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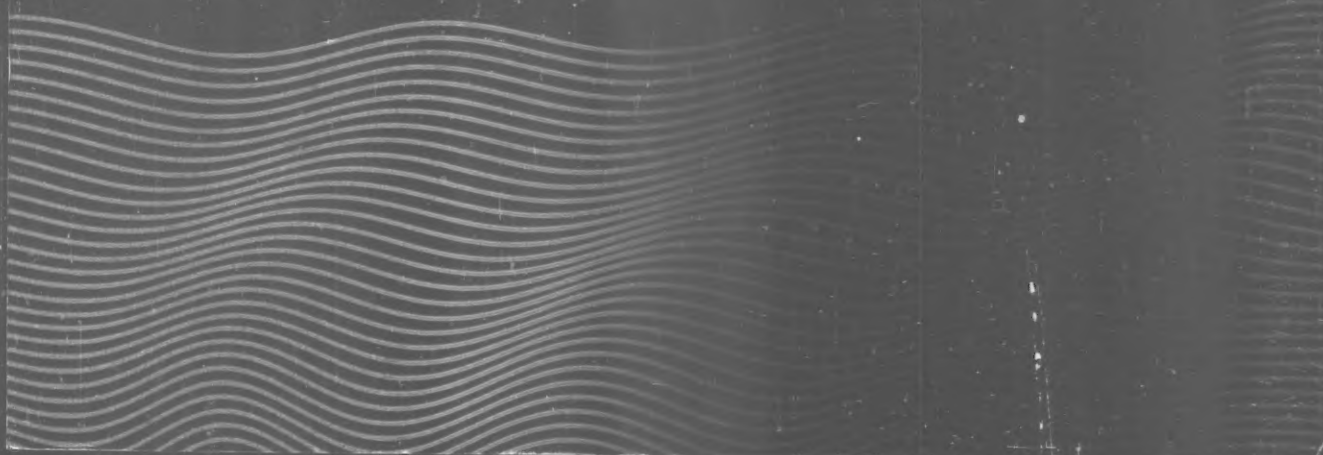
# Canadian Journal of Fisheries and Aquatic Sciences

# Journal canadien des sciences halieutiques et aquatiques



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Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37 et *Journal de l'office des recherches sur les pêcheries du Canada* 1938–79.

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# Canadian Journal of Fisheries and Aquatic Sciences

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# Fleet Dynamics and Individual Variation: Why Some People Catch More Fish than Others[1]

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Hilborn, R. 1985. Fleet dynamics and individual variation: why some people catch more fish than others. Can. J. Fish. Aquat. Sci. 42: 2–13.

Most fisheries problems arise from a failure to understand and manage fishermen, and that the study of fishermen should be a major part of fisheries research. The dynamic behavior of fishing fleets can be broken into four components: investment, movement, catching power, and discarding. The literature in each area is reviewed and the needed research described. The second part of this paper examines the causes and consequences of individual variation in catch in a commercial purse seine fishery and a recreational hook and line fishery. It is shown that the catch is highly concentrated in the recreational fishery with a small proportion of frequent anglers catching a large portion of the fish. Catch is more equitably distributed in the purse seine fishery. The consequence of individual variation includes the observation that small annual bag limits in the sport fishery could reduce the total catch significantly while leaving most anglers unaffected and the fact that buy back of the most successful vessels would reduce the commercial catch by relatively little.

La plupart des problèmes relatifs aux pêches résultent d'une incompréhension des pêcheurs et d'une mésentente avec ces derniers ; par conséquent, l'étude des pêcheurs devrait être une partie importante de la recherche sur les pêches. Le comportement dynamique des flottilles de pêche peut être divisé en quatre composantes : investissement, déplacement, potential de capture et rejet. L'autour évalue des ouvrages sur le sujet et décrit la recherche nécessaire. La seconde partie du présente document porte sur les causes et les conséquences de la variation individuelle des prises commerciales à la senne coulissante et les captures sportives à la ligne et hameçon. L'auteur démontre que les prises sont fortement concentrées dans la pêche sportive où un petit nombre de pêcheurs à la ligne capturent une grande partie des poissons. Dans la pêche à la senne coulissante, les prises sont plus équitablement réparties. L'auteur déduit de ces variations individuelles que des limites annuelles de capture en pêche sportive pourraient réduire le total des prises de façon significative tout en ne touchant qu'un petit nombre de pêcheurs et que le rachat des bateaux les plus rentables ne réduirait guère les prises commerciales.

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In 1982, the Pacific and Atlantic fisheries of Canada were widely recognized to be in crisis. This recognition led to the establishment of a Royal Commission on Pacific Fisheries Policy headed by Peter Pearse (Pearse 1982) and the Task Force on the Atlantic Fisheries headed by Michael Kirby (Kirby 1982). Both studies quickly discovered that the crises were indeed real and made strong recommendations for public expenditures of hundreds of millions of dollars.

Figure 1 shows the annual catch of salmon in British Columbia and of the northern cod stock in eastern Canada, which represent the major commercial species. Surprisingly, there has been no decline in salmon catches in British Columbia, and Canadian harvests of northern cod have been increasing. Both the Pearse and Kirby reports recognized that the crises were not due to a lack of fish, but instead to other factors such as overexpansions of fishing fleets and process facilities, poor prices, and escalating costs. Salmon and northern cod are, of course, not the only harvested species, and some specific fisheries have indeed seen drastic declines in catch (herring in eastern Canada for instance). It certainly appears that the crises in Canadian fisheries in the 1980s are not due to poor biological understanding of fish stocks, but rather to external factors and a failure to understand and manage fishermen.

Canada's situation is far from unique. Most major fishery problems in the world are due not to poor understanding or biological management of fish but to problems with fishermen. The collapse of the Peruvian anchoveta was not due to "el Niño", but rather to the inability of the Peruvian authorities and fishermen to reduce harvesting pressure after a period of poor recruitment and high vulnerability (Troadec et al. 1980). Biological warnings and recommendations were given well in advance (Glantz and Thompson 1981). There is little doubt that Peru could still have had a large sustained anchoveta harvest; instead, the stock was fished to commercial extinction. The Peruvians were deeply indebted for loans to develop their fishing fleet and processing facilities, and they considered it better to keep fishing to meet loan payments and the social goal of keeping fishermen employed.

The second great fishery tragedy of the last 20 yr is the collapse of Norwegian herring. This once magnificent stock

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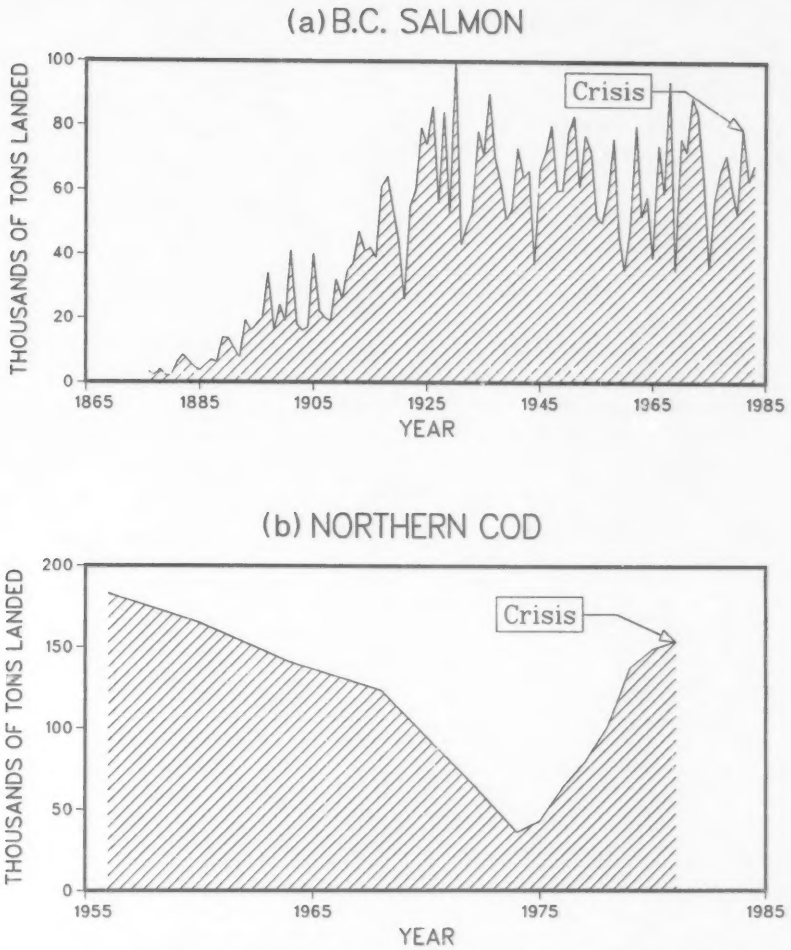


FIG. 1. Annual landings of (a) salmon in British Columbia from 1876 to 1983 and (b) northern cod in eastern Canada from 1955 to 1981. Northern cod data from Munro and McCorquodale (1981) and Kirby (1982).

declined from over 10 million tons in 1957 to 30 thousand tons in 1971 (Dragesund et al. 1980). The collapse was due to overfishing. The failure to reduce harvest rates as the stock collapsed can be ascribed to (1) misleading catch per effort that did not decline proportionately to stock size, (2) international disagreement over who should reduce catch, and (3) economic pressure on highly capitalized fleets. Again, the major biological element in understanding the Norwegian herring problems was the relationship between stock size and catch per effort, which requires an understanding of the fishing process and the spatial distribution of the fish. My point is that poor understanding of fish biology was not the cause of the Norwegian herring collapse.

This sad litany of fisheries disasters can be ascribed to poor understanding of the dynamics of fishermen, how they fish, and how they invest. I therefore argue that a major element of fisheries science should be the study of fishermen and fleet dynamics.

Figure 2 illustrates my conception of the four elements of fisheries — population dynamics, fleet dynamics, processing, and marketing — and how they interact. The fleet takes catch from population dynamics and inflicts mortality on the stock. The fleet transfers catch to processing facilities in return for money. Processing sells its products to marketing in return for money. Inside each element there are dynamics such as birth, death, investment, and depreciation.

I am certainly not the first to recognize that fisheries science includes more than the study of fish biology and population dynamics; however, it is frightening to look at university curricula and the scientific literature to see what is being done. Table 1 shows the distribution of main articles in volume 38 (1981) of the *Canadian Journal of Fisheries and Aquatic Sciences* (1981 was chosen at random). There were no articles on fleet dynamics, processing, or marketing. In Canada, as elsewhere, studies of fleet dynamics, processing, and marketing are not an integral part of fisheries science. This is not too surprising, because nearly all fisheries scientists are biologists trained in fishery biology. However, I have never yet had a conversation with a fisherman in which processing and marketing were not among the foremost concerns, and I conclude that we just do not know what kinds of questions to ask.

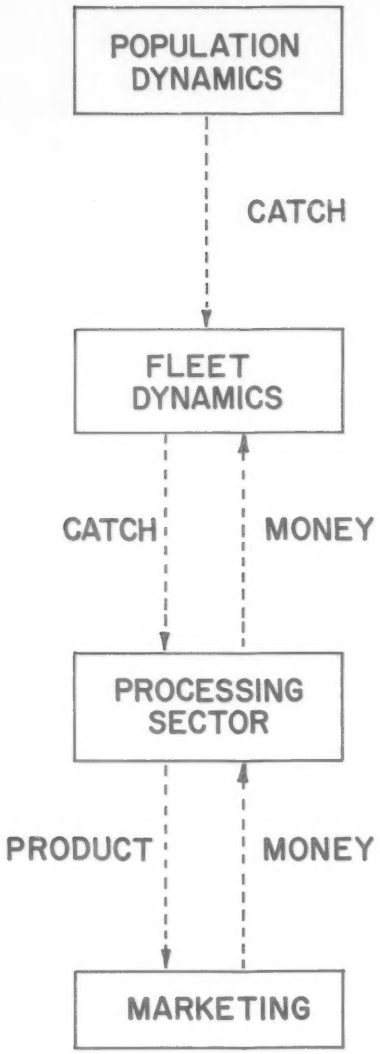


FIG. 2. Interaction between the four major elements in a fishery.

There is a widely cherished belief that once we step outside of fish population dynamics we have crossed into economics, and that problems of fleet dynamics, processing, and marketing should be left to economists. Two major objections come to mind why these topics should not be abandoned to economists. First, many of the important questions occur at the interface between fleet dynamics and fish biology. The relationships between catch per effort and fish abundance require looking at both the fish and the fishermen. Similarly, discarded by-catch and incidental mortality requires an understanding of fish behavior in relation to gear, as well as market pressures on fishermen and vessel operation.

Second, economists are not generally trained to study dynamic systems. The bulk of economic theory concerns itself with equilibrium conditions, and the economists' track record of understanding and managing the dynamic behavior of fishing fleets is just as bad as that of the biologists. Good work on fleet dynamics is now being done by biologists (Botsford et al. 1983), economists (Aranson 1984; Munro and McCorquodale 1981; Wilen 1976), mathematicians (McKelvey 1983; Clark and Lamberson 1982), and anthropologists (Smith 1974). The problems of fleet dynamics require a fundamentally ecological perspective, that is, how do fishermen interact with their environment (fish, markets, and other fishermen), and this perspective sometimes is found in anthropology and economics.

TABLE 1. Frequency of principal topics of relevant fisheries management articles appearing in volume 38 (1981) of the *Canadian Journal of Fisheries and Aquatic Sciences*.

| Topic | Number of articles |
|---|---|
| Fish biology | 49 |
| Population dynamics | 46 |
| Fleet dynamics | 0 |
| Processing | 0 |
| Marketing | 0 |
| Limnology/oceanography | 29 |

The next section of this paper concentrates on fleet dynamics, looks at the critical components of fleet dynamics, and discusses the types of research needed in each. The paper then presents some results from studies my students and I have done on one aspect of fleet dynamics: the causes and consequences of individual variation in catch.

## Elements of Fleet Dynamics

This section presents a classification of the elements of fleet dynamics, recognizing that other scientists, approaching the study of fleet dynamics from a different perspective, might choose a different classification scheme.

The four elements of fleet dynamics are (1) investment/disinvestment: birth, aging, and death of fishing vessels; (2) effort allocation: when to fish, where to fish, and what to fish for; (3) harvesting efficiencies: the elements of the fishing process, competition, interference, facilitation, and learning; and (4) discarding and keeping: the choice of what to keep and what to let go. These elements are summarized in Table 2.

Studies of fleet dynamics can be roughly divided into two types: those that analyse the optimum or theoretical behavior and those that examine data to see if the real fishermen behave the way theory says they should. There has been remarkably little theory developed in fleet dynamics, and this has probably inhibited the analysis of data beyond a rather trivial descriptive stage.

### Investment/Reinvestment

Most major fisheries problems are partially caused by overinvestment. The classic paper by Gordon (1954) explains with a simple equilibrium model why this happens. The dynamics of investment can first be approached by a simple breakdown of the component processes associated with changes in the capital stock of the fishing fleet:

$$(1) \quad C_{t+1} = C_t - L_t + I_t - D_t + M_t$$

where $C$ is capital invested in the fishery, $L$ is losses in the form of sinkings, scrappings, or transfer of vessels to different fisheries, $I$ is investment in new vessels or transfers from other

TABLE 2. Principle element of fleet dynamics.

| | |
|---|---|
| I. | Investment and fleet size |
| | (a) Loss of vessels due to sinking, scraping, or transfer to other fishermen |
| | (b) Depreciation of existing fleets |
| | (c) Acquisition of new vessels by construction or transfer from other fisheries |
| | (d) Maintenance and upgrading of existing vessels |
| II. | Effort allocation |
| | (a) When to fish; what proportion of possible fishing times to utilize |
| | (b) Choice of areas to fish in |
| | (c) Choice of species to target on or gear to use |
| III. | Harvest efficiency |
| | (a) Relationship between vessel attributes, crew, gear, and relative catching power |
| | (b) Functional time budget analysis of catching process |
| | (c) Relationship between total effort, abundance, and catch |
| IV. | Discarding and by-catch |
| | (a) Relationship between what comes in the net and what is kept |

fisheries, $D$ is depreciation due to normal vessel operation and use, and $M$ is maintenance repairs and expenditures.

The theory of optimal fisheries investment has been extended to dynamics situations by Clark et al. (1979) and Charles (1983a, 1983b). All of these studies examined investment and harvest policies as a function of stock size and fleet size. The extent to which surplus fishing vessels could be sold had a profound influence on the conclusions; investment should be more conservative and overexploitation will be more common when there is little market for surplus vessels.

There is remarkably little work done on what determines investment and disinvestment. Wilen (1976) and Gatto et al. (1975) used aggregate models that considered a proportion of past profits to be reinvested. When profits are good the fleet grows, and when they are negative the fleet shrinks.

With his model, Wilen (1976) explored how fishermen entered and left the North Pacific fur seal fishery in the late nineteenth century. Gatto et al. (1975) were less successful with a number of groundfish stocks. Botsford et al. (1983) examined entrance and exit for the California Dungeness crab (*Cancer magister*) fishery and found that there was entry when fishing was good and exit when it was poor, but they did not look at the relationship between entry, exit, and stock levels. Clark and Lamberson (1982) analyzed the pelagic whaling industry after 1945 and showed that investment and overharvesting could be explained by the economics of the fishery operation and the slow growth rate of whale populations. A nondynamic, but very interesting study by Clark and Kirkwood (1979) examined investment levels in relationship to profits in Gulf of Carpentaria prawn vessels and found that the observed fleet size was roughly similar to that predicted by an equilibrium analysis.

There are no studies that directly examine investment in new vessels and entrance from other fisheries, disinvestment, depreciation, and maintenance in relation to fleet size, catches, and profitability. Aranson (1984) has shown that vessel loss from the Icelandic demersal fleet consists of a constant age-independent mortality rate due to sinkings, and an accelerated mortality of older ages presumably due to scrapping. I can find no paper that has data relating profits to the number of vessels entering the fishery, something that surely could be done for certain fisheries.

The first question to ask is the relationship between investment and profits. When fishing is highly profitable, how fast do new vessels enter? In many fisheries, external factors such as other fisheries and subsidies may have an important impact, and investment may be only weakly related to profitability. If we do find a relationship between profits and investment, we then need to determine if past profits or anticipated profits drive investment. Do individual investors make myopic decisions assuming no one else will invest, or are fishermen investing in boats because it is an industry in which they understand the risks and potential yields? Alternatively, do fishermen invest profits in other forms of investment?

Understanding the investment process is probably the most important area for research in fisheries, and yet there is a mere handful of papers on the topic. The data are often difficult to obtain, but this type of study should receive the highest priority.

## Effort Allocation

Given a fleet size determined by investment dynamics, the next component of fleet dynamics is the determination of fishing effort, which again has three separate components: (1) when to fish, (2) where to fish, and (3) what to pursue. In some fisheries the seasons are so short that each vessel literally fishes for the entire permissible season. More often, though, fishermen must make some choices of when to fish, either because it may be unprofitable to go fishing because of poor weather, or because of better alternative uses of time. When Millington (1984) plotted the number of gillnet vessels operating in British Columbia against the catch per boat the previous week (Fig. 3), he found that when fishing is poor, most fishermen will not go fishing. The distribution of percent of vessels operating at different levels of income likely reflects a distribution of variable costs, the desire to test gear before the main fishing season, and exploratory fishing to determine stock abundance.

Further studies could examine many fisheries to determine the extent to which weather, past catches, or even months of the year influence fishing effort. Numerous data bases based on log books exist that could easily be used for such studies.

Fishermen generally have a choice of fishing locations, and the next logical type of study is to determine where vessels will go. Hilborn and Ledbetter (1979) have shown that British Columbia salmon seiners move to where fishing is good, but catch per vessel is systematically higher in some areas than in others. Liao (1979) has shown that the mobility of shrimp vessels in the South Atlantic states is largely determined by the size of vessels, alternative employment for skippers, and success rates in different fisheries. The simplest starting assumption for studies of effort allocation would appear to be that vessels will move to equalize catch per boat, but there are so many individual factors in each fishery that this simple rule may rarely hold true.

The third part of effort allocation is species target and/or gear choice. In many fisheries, several species are fished with either the same or alternative gear. A starting hypothesis might be that species will be taken in relation to their abundance, yet it seems more likely that price or processor's demand will greatly determine the target species. A data base on catches and abundance in an area would enable one to ask about species targeting, yet I know of no literature on the subject.

## Harvest Efficiency

The best studied area in fleet dynamics has been the analysis

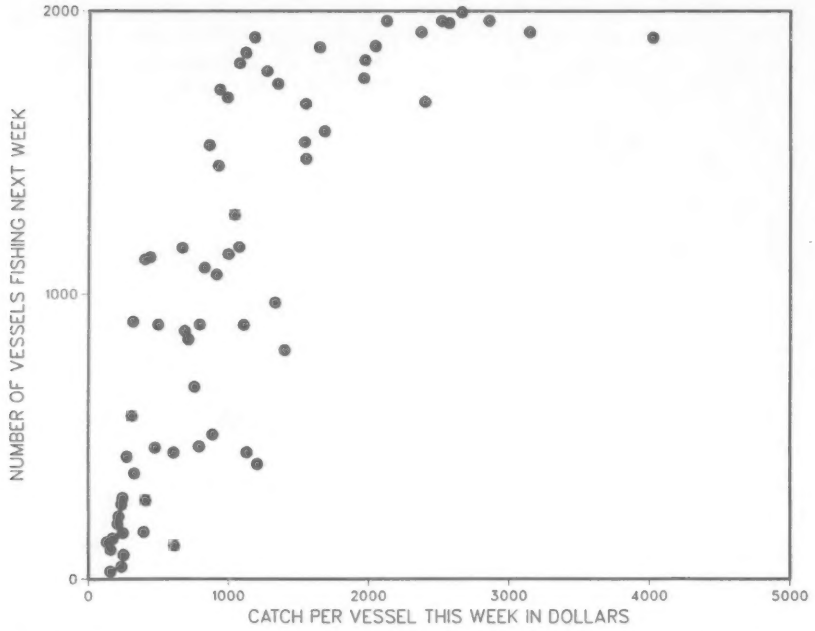


FIG. 3. Number of British Columbia gillnet fishermen fishing plotted against the average catch per boat the previous week. Data from 1979–81 included. Redrawn from Millington (1984).

of harvest efficiency of individual vessels or aggregate fleets. Two approaches have emerged: the statistical approach relates vessel attributes, gear, and crew levels, and a functional approach looks more deeply into the components of the harvesting process, such as time spent in different activities and area swept by gear.

The majority of efficiency studies relate vessel attributes to catch level, usually by multiple regression. Gulland (1956) found a good relationship between tonnage and fishing power for the English demersal fleets operating on many species, whereas Houghton (1977) found little relationship between any vessel attribute and fishing power on the same species. Hilborn and Ledbetter (1985) found that some salmon purse seiners were repeatedly better than others but found no relationship between fishing power and vessel attributes, and they suggested that the repeatable differences are due to skippers. Pálsson and Durrenberger (1982) found no evidence for a skipper effect in an Icelandic fishery. The symposium edited by Pope (1975) includes numerous papers dealing with this topic. These studies are typical of the rather mixed results obtained from examination of the relationship between vessel performance and specific vessel characteristics.

The functional approach to harvesting efficiency investigates the components of the fishing process and fishing gear and how they interact with the fish to determine catch. The classic catch equation is

$$C = NEq \quad (2)$$

where $C$ is catch, $N$ is abundance of fish, $E$ is effort, and $q$ is the proportion of the stock captured by one unit of effort. A first step in a functional approach, based on the early work of Paloheimo and Dickie (1964), examines the catching process in more detail, for example with the following model:

$$C = \frac{vpD}{1 + hvpD} \quad (3)$$

where $C$ is the catch, $v$ is the volume of habitat searched, $p$ is the probability that a fish (or school) will be captured if it is in the searched area, $D$ is the density of fish, and $h$ is the handling time (nonsearch) per fish (or school) captured. Modifications of equation 3 are appropriate for highly aggregated species but the equation gives us a mechanistic framework to analyze vessel attributes, fishermen's decisions, and fish behavior. For instance, $v$, the volume searched, is in itself related to the speed of search, the area swept, and the reliability of the detecting device. Technological change in the form of faster boats to increase speed and higher towers or better electronics to increase area swept can easily be related to catching power. General search efficiency in fisheries has been studied recently by Mangel and Clark (1983). The probability of attack, $p$, can be related to species price and density of alternative species. The handling time, $h$, can be reduced by technological innovation and is greatly affected by skipper skill. These functional studies generally require time budgets made by on-board observers, and although I know of no published results from such a study, there are several currently underway or being written up.

When such detailed time budgets are not available, one can often look at the relationship between fish abundance and catch. Figure 4 shows such a graph from Peterman (1980) for a subsistence fishery. The reduced harvest rate at higher abundance could be due to many factors such as less fishing time when catches are good, handling time using up most of the available fishing time, or changing fish behavior, but in the absence of detailed data we cannot distinguish between these alternatives. However, for purposes of management it may not ben necessary to determine why the graph looks the way it does.

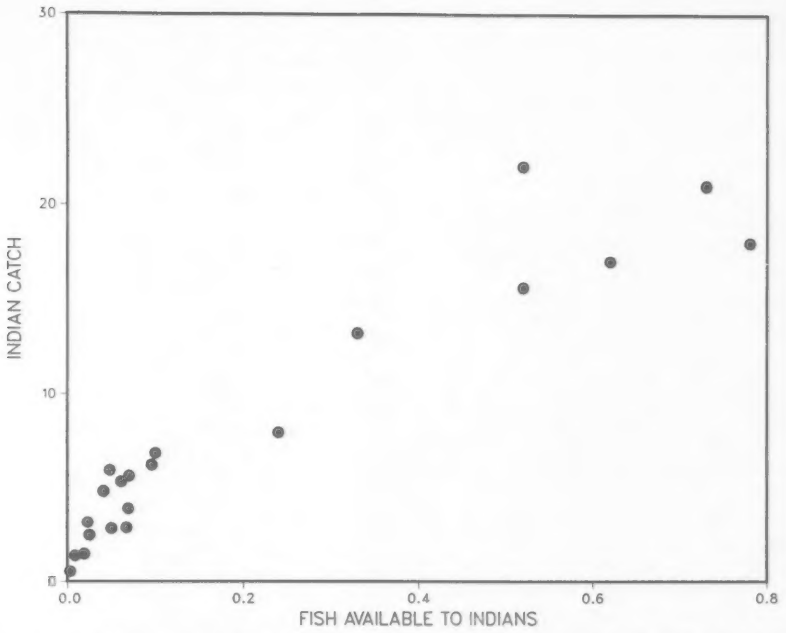


FIG. 4. Total Indian food fishery catches of Stuart River sockeye salmon in relation to abundance. Redrawn from Peterman (1980).

Studies of harvest efficiency should also include analysis of vessel competition for physical access or information, facilitation between individual vessels by information sharing, and active interference through disinformation or mischief.

The ultimate objective of harvest efficiency studies is to determine how fish abundance and effort affect catch. When catch per unit effort is used to determine fish abundance, then such an understanding is absolutely essential to determine stock size and harvest potential.

### Discarding and Incidental Fishing Mortality

Discarding and incidental fishing mortality are of great concern in many fisheries. Discarding is a particular problem, since it may be illegal, and yet there can be strong economic pressure to sort for size or species. Detailed on-board studies to find out when fishermen will discard fish are probably the only answer. A serious concern regarding proposed individual vessel quotas in many fisheries is that there will be a strong incentive to keep only the highest quality or largest fish. For instance, it is widely believed that Alaska troll fisheries adopted an informal size limit considerably greater than the legal size limit when a catch ceiling was imposed in 1983 and 1984. There is an increasing body of literature on by-catch and discarding (e.g. IDRC 1982) but in the absence of any theory, these studies lack any direction.

## Causes of Individual Variation in Catch

Having reviewed the major areas of fleet dynamics, I would now like to look at one specific aspect of fleet dynamics: individual variation in catch. We all know that some fishermen catch more than others, but I know of no one who has systematically explored the causes and consequences of such individual variation. This portion of the paper examines the variation in catch in a commercial fishery (British Columbia salmon seiners) and a recreational fishery (British Columbia salmon sports fishermen). I shall look at the amount of variation, the causes of such variation, and the management and policy consequences of variation in catch.

### The Fisheries

For the last decade the British Columbia salmon seine fishery has consisted of roughly 525 drum seiners. Fleet size has remained quite stable during this period due to license limitation. The analysis presented below is based on the landing records maintained for each vessel by the Department of Fisheries and Oceans (DFO). The catch records contain the location fished, number and weight of fish by species, and landed value at each time of sale.

Purse seiners almost universally sell fish once a week, and since most British Columbia salmon seine fisheries begin at 6 p.m. Sunday and last for 1–3 d, I have used the dollars per week as the basic unit of catch. Location is recorded as one of 30 statistical areas on the British Columbia coast. Thus for each vessel, there are weekly records of where it fished and what it caught. A more detailed description of the data can be found in Hilborn and Ledbetter (1979, 1985).

The British Columbia salmon sport fishery takes place year round predominantly in the Strait of Georgia between Vancouver Island and the mainland. DFO has conducted a logbook program among approximately 2000 sport fishermen (Bijsterveld 1983). Data for each trip specify the number of hours fished, number of lines employed, location fished, and number of fish caught and kept by species and size. Both fisheries fished in the same statistical areas.

## Determinants of Catch

The standard fisheries catch equation is

(4) Catch = Abundance × effort × catching power

or

$$C = NEp.$$

Thus, a fisherman who catches more fish than average may do so because he goes where there are more fish ($N$ is large), goes more often ($E$ is large), or has a higher catching power than other fishermen ($p$ is large). $N$ incorporates both abundance and vulnerability. We can examine the total variation in catch for our two fisheries and see how it is related to the variation in each of the three components.

In the salmon purse seine fishery we can measure effort as the number of weeks fished. Abundance is calculated as an average value per week among all boats in each area a boat fished. This assumes that the average dollars per week obtained by all seine boats in an area in a week is a measure of abundance. In fact, although income is a measure of abundance, price, species composition, and fish vulnerability, these are precisely the important factors that are independent of an individual vessel, and are the best measure of "economic abundance." Since we measure catch in dollars per week, and fish abundance, price, species composition, and vulnerability are involved in this number of dollars per week, our measure seems appropriate. An individual vessel that has a low measure of abundance has unfortunately fished in poor areas; a vessel with a high measure of abundance has been in the right places at the right time. We have no independent way of measuring $p$, an individual vessel's catching power. However, we can rely on equation 4 to calculate $p$ as

$$(5) \quad p = \frac{C}{NE}$$

Thus, for each vessel we calculate its catching power by dividing its total catch (in dollars) by the number of weeks fished times the average dollars per week in the week/area stratum fished by that vessel. If $p > 1$, it means that the boat's catch was greater than the average catch per week in the week/area stratum it fished, and therefore it means the boat was more effective or luckier.

It should be noted that a more realistic version of equation 2 would add stochastic effects to the catch process, possibly of the log normal form:

$$(6) \quad C = NEpe^{v}$$

where $v$ is normally distributed with mean 0 and standard deviation $\sigma_v$. Thus, equation 5 becomes

$$(7) \quad pe^{v} = \frac{C}{NE}.$$

This is a formalization of our previous statement; a high $p$ may mean a luckier boat instead of a more effective one. Gulland (1956) used this same relationship although he separated vulnerability and density of fish into separate elements, whereas $N$ in equations 5–7 is the product of density and vulnerability. Gulland (1956) also refers to $p$ as fishing power.

Figure 5 shows the distribution of total catch (panel a), week fished (panel b), average abundance (panel c), and catching power (panel d) for 1980 in the British Columbia salmon purse seine fleet. It is readily seen that there is considerable variation in all factors, but that, contrary to popular beliefs, the distribution of catch is reasonably symmetrical. Table 3 shows a correlation matrix of catch, average abundance, weeks fished, and $p$. There are no strong correlations between the individual components, but not surprisingly, each component is correlated to total catch. We can examine the contribution to variation by noting that equation 4 can be rewritten as

$$(8) \quad \ln(C) = \ln(N) + \ln(E) + \ln(p)$$

and therefore, that if there are no correlations between $N$, $E$, and $p$, the variance of $\ln(C)$ should be the sum of the variances of the right-hand elements of equation 8. I have normalized $C$, $N$, $E$, and $p$ by dividing by their means so that the variance will be comparable. Table 4 shows the variance of the logarithm of the components; note that the variance of the right-hand elements of equation 7 do roughly sum to the variance of the left-hand side of equation 7.

Also note that the components are of approximately the same magnitude. Variation in $p$ appears to contribute most to the variance in catch, which can be explained by arguing that in the seine fishery everyone fishes almost anytime there is fishing to be done and mobility is high enough that few vessels will stay in bad places. Thus, it would follow that individual skill is the dominant factor in variation in catch. However, since $p$ as estimated by equation 7 also contains the stochastic element, it could also be argued that random chance is the major determinant of catch. Hilborn and Ledbetter (1985) have shown that about two thirds of the variation in $p$ is due to chance (the other one third due to skill and equipment). Consequently, I believe that the best interpretation is that the variation in catch among purse seines is determined by effort, abundance, $p$, and chance, with no individual factor dominating.

Figure 6 shows the distribution of catch, effort, abundance, and catching power for the British Columbia salmon sport logbook fishermen. Catch is measured in fish kept, effort in line hours, and abundance in average catch per line hour of all boats fishing the month/area stratum. Parameter $p$ is calculated according to equation 5. The catch distribution is much more skewed, since the majority of fishermen catch few fish, whereas a few catch a large number of fish. The distribution of catch can be seen to be largely due to the variation in effort, and contrary to my preconceptions there is no large tail of highly efficient fishermen. Table 5 shows the cross-correlation of the factors. The strongest correlation in catch is with effort. Surprisingly there is no major correlation between effort and $p$; yet there is a widely held belief that fishermen who go often are more effective. Table 6 shows the variances of the normalized variable. Variation in effort is over twice as important as variation in abundance or $p$. Since $p$ also contains the random error term, it seems reasonably clear that individual variation in $p$ is rather unimportant in the sport fishery.

Another interesting way of examining the distribution of catch and comparing it between the two fisheries is a concentration profile as shown in Fig. 7. The sport fishery is shown with a thick line and the seine fishery with a thin line. The concentration profile is generated by starting with the most successful fisherman and plotting the percent of total catch against the percent of the fishing population, and then doing the same for the top two fishermen and proceeding from best to worst fishermen. This graph reveals in a different way what we saw before, that a few sport fishermen take most of the sport catch whereas catch is more equally divided in the commercial fishery.

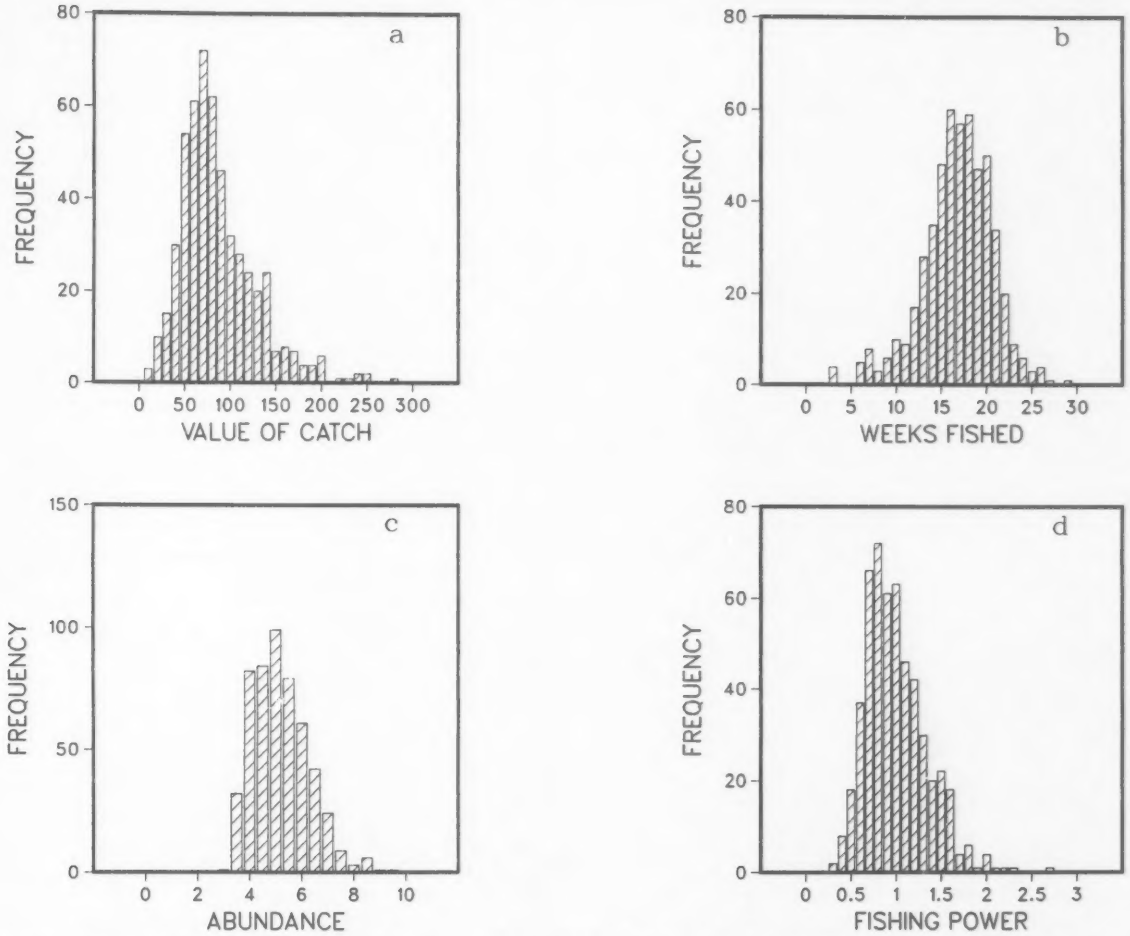


FIG. 5. Distribution of catch, effort, average abundance, and catching power in the British Columbia salmon purse seine fishery in 1980. (a) Relative frequency histogram of total landed value for the year; (b) relative frequency histogram of the number of weeks fished; (c) relative frequency histogram of the average catch per boat in areas fished; (d) relative frequency histogram of the catching power.

TABLE 3. Correlations between total value of catch, weeks fished, average abundance, and catching power for British Columbia salmon purse seiners.

| | Total value of catch | Weeks fished | Average abundance |
|---|---|---|---|
| Total value of catch | | | |
| Weeks fished | 0.50 | | |
| Average abundance | 0.37 | −0.13 | |
| Catching power | 0.73 | 0.02 | 0.05 |

TABLE 4. Variances of component of individual variation in catch in British Columbia salmon purse seine. Natural logarithms of normalized variables are used.

| Component | Variance |
|---|---|
| Effort | 0.09 |
| Average abundance | 0.04 |
| Catching power | 0.12 |
| Sum of above | 0.25 |
| Total value of catch | 0.25 |

## Consequences of Individual Variation

Having looked at the causes of individual variation, I now examine its consequences on fishing dynamics and regulation. There has been little work in this field; the fisheries literature deals mostly with average vessels. I will not provide a complete analysis of all the consequences of individual variation, but rather will highlight some of the more interesting implications in hopes of stimulating deeper research on the topic.

### Commercial Fisheries

A fisherman who wishes to do well in the British Columbia seine fishery could adopt, in principle, four strategies. He could specialize in one area, learn local tides, currents, and reefs, and become one of the best fishermen there. He could specialize in moving between areas so that he would always be where the best

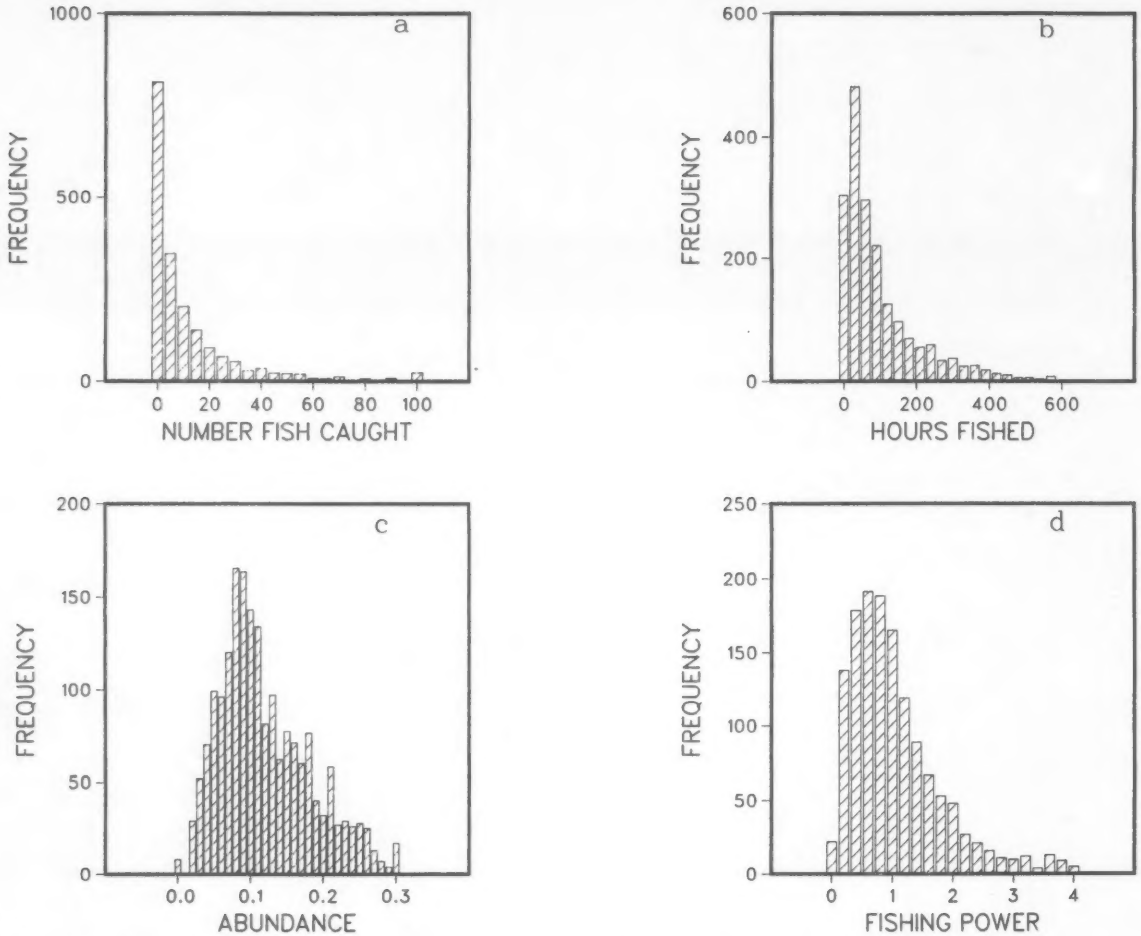


FIG. 6. Distribution of (a) catch, (b) effort, (c) average abundance in areas fished, and (d) catch power in the British Columbia salmon sport fishery.

TABLE 5. Correlation between number of fish kept, fishing effort, average abundance, and catching power for British Columbia salmon sport fishermen.

| | Number kept | Effort | Average abundance |
|---|---|---|---|
| Number kept | | | |
| Effort | 0.65 | | |
| Average abundance | 0.22 | −0.03 | |
| Catching power | 0.27 | 0.02 | −0.06 |

TABLE 6. Variances of components of individual variation in catch in British Columbia salmon sport fishery. Natural logarithms of normalized variables used.

| Component | Variance |
|---|---|
| Effort | 1.19 |
| Average abundance | 0.25 |
| Catching power | 0.75 |
| Sum of above | 2.19 |
| Total number of fish kept | 1.61 |

fishing was to be found each week. He could buy as good a boat as possible to maximize his catching power wherever he fished. Finally, he could just fish as often as possible.

Of these four possible strategies, only the first two are really viable. Hilborn and Ledbetter (1985) have shown that physical attributes of vessels do not relate to catching power to any major degree; thus, catching power cannot be "bought" in the form of a good boat. There are so few opportunities to seine for salmon in British Columbia that most boats fish almost every week. However, two "more fishing" strategies are appearing on a smaller time scale. These involve fishing more hours per day. Some fishermen now fish 24 h a day when the fishery is open. Another "more fishing" strategy is to start fishing in one area, and then move to another if fishing appears to be better at the other location.

The two successful strategists are the area specialist who attempts to maximize $p$ and the movement specialist who

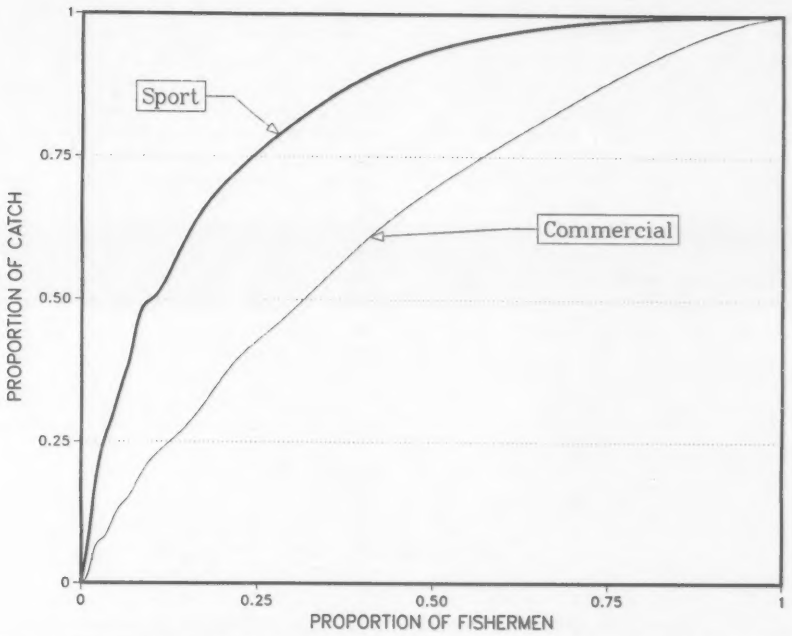


FIG. 7. Concentration profiles for the 1980 British Columbia salmon purse seine fleet (thin line) and the 1982 British Columbia salmon sport fishery (thick line).

attempts to maximize *N*. Both types are found in the British Columbia salmon seine fleet. Present regulation proposals aimed at vessel reduction (buy backs) could be fruitless if the low catch vessels are bought out, since there would not be that many more fish to share among the remaining boats. A more knowledgeable reduction program might want to buy back the most successful vessels, an apparently clever move. However, once we recognize that the successful fishermen are successful because of area knowledge and skill, we realize that buy back of successful vessels is not the answer. The most successful fishermen would need to leave the fishery to greatly increase the catch available to the remaining fishermen.

Another current proposal for fisheries regulation is area licensing. Such a regulation will obviously be to the detriment of a fisherman who specializes in moving between areas. The presence of a large number of such area specialists in the British Columbia salmon fleet has led to strong opposition to area licensing by many individuals and groups of fishermen. Many fishermen have devoted years to learning which weeks are best for which areas, and area licensing would deny them the opportunity to use that information to their advantage.

Individual variation also affects distribution of profits at bionomic equilibrium. Traditional economic theory suggests that investment will flow into the fishery until profits reach zero. If there is individual variation in catch and the source of the variation is not related to the level of investment (demonstrated in Hilborn and Ledbetter 1985), then the better fishermen will be making a profit at equilibrium. Poor fishermen would presumably either leave the fishery or accept a lower return for their labor. Indeed, individual variation in the evaluation of opportunity cost of their own labor is a major feature of many fisheries. If we accept that under most circumstances some fishermen will always be able to make a profit, we will then want to know what becomes of this profit. Do the fishermen invest it in their own vessel, buy other vessels with less skilled operators, or invest it outside the fishery? These are some very critical questions to which answers are needed to understand investment dynamics. Without looking at individual variation, it may be impossible to understand investment dynamics.

A final consequence of individual variation is the effect highly skilled individuals have on the harvesting capability of less skilled fishermen. Studies of foraging in flocking birds (Thompson et al. 1974) have shown that efficient searching by one individual can improve the foraging efficiency of a flock of birds. Similarly, we might well expect many less skilled fishermen to imitate or follow the fishing pattern of the more successful ones, and thus a few skilled or innovative individuals may greatly change the harvesting capacity of the entire fleet.

## Sport Fishery

Sport fisheries stand in great contrast to commercial fisheries. The traditional nemesis of commercial fisheries, overcapitalization and inefficiency, are valued aspects of a recreational fishery. It is often said that a perfect recreational fishery is one that has enormous effort and no catch. This is unfortunately far too often the case for commercial fishermen. The concentration profiles in Fig. 7 illustrate a major difference between the two fisheries. Catch in the sport fishery is far more concentrated, and the major cause of this concentration is variation in effort. An avid sports fisherman can fish hundreds of days per year, whereas most casual anglers fish only a few days per year.

A contentious issue in the British Columbia sport fishery has been annual bag limits designed to reduce the catch of the very frequent fishermen. Proposed regulations of annual bag limits that would affect less than 5% of anglers have been strongly opposed by sport fishing groups. This seems to be due to two factors. First, the most active fishermen spend disproportionate

amounts of time fishing (that is why they catch the fish), and therefore have a much bigger stake in the fishery. Second, the type of person who takes an active role in a fishing interest group very likely is a frequent fisherman and associates with other frequent fishermen. Thus, the few fishermen who would be affected by small annual bag limits are the same people one expects to lead fishermen lobby groups.

This is not intended as a criticism of the role such active fishermen play, since one could argue that these fishermen should be the major client group because recreational fishing is such a dominant part of their lives. Individual variation in effort and catch is simply one aspect of recreational fishing we need to live with and try to accommodate. The sports fishery is a heterogeneous group of people with vastly different motivation and interests.

## Research and Data Needs

The purpose of this paper has been to highlight the importance of fleet dynamics in fisheries and to demonstrate that the relevant questions in fleet dynamics can be treated as ecological problems. The review of the components of fleet dynamics outlined the important questions in each area and suggested methods for comparing alternative hypotheses. The final sections on causes and consequences were included to show some substantial results of fleet dynamic studies, and to demonstrate how existing data bases can be used to ask many of the relevant questions. Many important studies can be done in very little time when the data have already been collected. Only 10 h at a computer terminal was spent to get the results on individual variation presented in this paper. Many researchers now have data bases available to them and should be ready to ask such questions. I hope that this paper will motivate them to look at the data they have. Clearly, in many cases new data must be acquired, and we now understand the types of data needed.

Large-scale patterns of investment, particularly entry of new vessels, can be examined from data bases on vessel landings and value of landings, which are standard data bases currently available for Canada and for most of the world's major fisheries. No new data collection is required. It is typically more difficult to determine actual profits. While value of catch is often easily obtained, costs are more difficult to find, although aggregate cost figures can often be estimated.

Individual cost and landings figures are much harder to find. One DFO study in British Columbia has obtained anonymous income tax records from fishermen's accountants, giving vessel-by-vessel costs, incomes, and investments for a period of 10 yr. These are relatively difficult data to get, but I have been surprised how often fishermen have offered to open their books and I suspect that a bit of creativity, such as exhibited in the British Columbia study, will reap great rewards.

Effort dynamics are reasonably easy to study when catch and effort statistics are available. When location fished is also available, movement patterns can be examined. In the absence of individual vessel catch records, one cannot look at the movement patterns of individual boats. However, the type of movement dynamics studies of Hilborn and Ledbetter (1979) and Millington (1984) do not require individual vessel statistics.

The general relationship between effort, fish abundance, and catch can be studied at an aggregate level when catch and effort are available. For many species, virtual population analysis (VPA) is available to provide fish abundance, and studies such as Peterman (1980) can be performed from such data.

Functional analyses of vessel operations require on-board observations or detailed logbooks. It is surprising how many such data bases are currently available or could be collected using existing observer programs. Time budgets are the most useful type of data for quantifying the elements of travel, search, and capture but require an on-board observer, since fishermen are usually too busy fishing.

Studies of discarding behavior could presumably be done by recording for an individual vessel all fish captured by gear type and the proportion of each species, size, or quality class retained. The reliability of logbook data on discarding would certainly be questionable, and even on-board observer records would be subject to the assumption that fishermen behave the same with or without an observer. Nevertheless, it is such an important question that preliminary studies should be begun. Incidental mortality inflicted by gear but never brought on board is even more difficult to study, and the details of such a study would differ enormously from fishery to fishery.

## Conclusion

Fleet dynamics should be an explicit part of any fisheries curriculum or research program. The types of questions to ask are well understood, and the data are either available or readily collected. We now need a commitment from administrators to fund such programs and the desire of scientists to do the work.

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## References

ARANSON, R. 1984. Efficient harvesting of fish stocks: the case of Icelandic demersal fisheries. Ph.D. thesis, Department of Economics, University of British Columbia, Vancouver, B.C.

BIJSTERVELD, L. 1983. The B.C. tidal water sportfishing diary program. 1981. Can. MS. Rep. Fish. Aquat. Sci. 1717.

BOTSFORD, L. W., R. D. METHOT JR., AND W. E. JOHNSTON. 1983. Effort dynamics of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 40: 337–346.

CHARLES, A. T. 1983a. Optimal fisheries investment: comparative dynamics for a deterministic seasonal fishery. Can. J. Fish. Aquat. Sci. 40: 2069–2079.

1983b. Optimal fisheries investment under uncertainty. Can. J. Fish. Aquat. Sci. 40: 2080–2091.

CLARK, C. W., F. H. CLARKE, AND G. R. MUNRO. 1979. The optimal exploitation of renewable resource stocks: problems of irreversible investment. Econometrica 47(1): 25–47.

CLARK, C. W., AND G. P. KIRKWOOD. 1979. Bioeconomic model of the Gulf of Carpentaria Prawn Fishery. J. Fish. Res. Board Can. 36: 1304–1312.

CLARK, C. W., AND R. LAMBERSON. 1982. An economic history and analysis of pelagic whaling. Marine Policy April 1982, p. 103–120.

DRAGESUND, O., J. HAMRE, AND O. ULLTANG. 1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 43–71.

GATTO, M., S. RINALD, AND C. WALTERS. 1975. A predator–prey model for discrete-time commercial fisheries. International Institute for Applied Systems Analysis, Laxenburg, Austria, Research Report 75-5.

GLANTZ, M. H., AND J. D. THOMPSON [ED.] 1981. Resource management and environmental uncertainty: lessons from coastal upwelling fisheries. John Wiley & Sons, New York, NY. 491 p.

GORDON, H. S. 1954. The economic theory of a common-property resource: the fishery. J. Polit. Econ. 62: 124–142.

GULLAND, J. 1956. On the fishing effort in English demersal fisheries. *In* Fishery investigations. Ser. 1. Vol. V. Ministry of Agriculture, Fisheries and Food, London.

HILBORN, R., AND M. LEDBETTER. 1979. Analysis of the British Columbia salmon purse-seine fleet: dynamics of movement. J. Fish. Res. Board Can. 36: 384–391.

1985. Determinants of catching power in the British Columbia salmon purse seine fleet. Can. J. Fish. Aquat. Sci. 42: 000–000.

HOUGHTON, R. G. 1977. The fishing power of trawlers in the western English Channel between 1965 and 1968. J. Cons. Int. Explor. Mer 37: 130–136.

IDRC. 1982. Fish by-catch ... Bonus from the sea. 1982. Report of a Tech. Consultation on shrimp by-catch utilization held in Georgetown, Guyana, 27–30 Oct. 1981. IDRC, Ottawa, Ont. 163 p.

KIRBY, M. 1982. Navigating troubled waters: a new policy for Atlantic fisheries. Report of the Task Force on Atlantic Fisheries, Ministry of Supply and Services, Ottawa, Ont.

LIAO, D. S. 1979. An economic analysis of mobility of shrimp vessels in the South Atlantic states. South Carolina Wildl. Mar. Resour. Dep. Tech. Rep. 35.

MANGEL, M., AND C. W. CLARK. 1983. Uncertainty, search, and information in fisheries. J. Cons. Int. Explor. Mer 41: 93–103.

MCKELVEY, R. 1983. The fishery in a fluctuating environment: coexistence of specialist and generalist fishing vessels in a multipurpose fleet. J. Environ. Econ. Manage. 10: 287–309.

MILLINGTON, P. 1984. The fishermen as predator: numerical responses of British Columbia gillnet fishermen to salmon abundance. M.Sc. thesis, Department of Zoology, University of British Columbia, Vancouver, B.C.

MUNRO, G. R., AND S. MCCORQUODALE. 1981. The northern cod fishery of Newfoundland. Economic Council of Canada Technical Report No. 18.

PALOHEIMO, J. E., AND L. M. DICKIE. 1964. Abundance and fishing success. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 155: 152–163.

PÁLSSON, G., AND P. DURRENBERGER. 1982. To dream of fish: the causes of Icelandic skippers' fishing success. J. Anthropol. Res. 38: 227–242.

PEARSE, P. 1982. Turning the tide, a new policy for Canada's Pacific fisheries. Department of Fisheries and Oceans, Ottawa, Ont. 292 p.

PETERMAN, R. M. 1980. Dynamics of native Indian food fisheries on salmon in British Columbia. Can. J. Fish. Aquat. Sci. 37: 561–566.

POPE, J. A. [ED.] 1975. Measurement of fishing effort. Meeting held at Charlottelund Slot, Charlottelund, 25 and 26 Sept., 1970. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 168.

SMITH, C. L. 1974. Fishing success in a regulated commons. Ocean Dev. Int. Law J. 1(4): 369–381.

THOMPSON, W. A., I. VERTINSKY, AND J. KREBS. 1974. The survival value of flocking in birds: a simulation model. J. Anim. Ecol. 43: 785–820.

TROADEC, J.-P., W. G. CLARK, AND J. A. GULLAND. 1980. A review of some pelagic fish stocks in other areas. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177: 252–277.

WILEN, J. E. 1976. Common property resources and the dynamics of overexploitation; the case study of the North Pacific fur seal. Univ. B.C. Programme Nat. Resour. Manage. Resour. Pap. No. 3. 49 p.

# Growth of the Euphausiids *Thysanoessa inermis*, *Thysanoessa raschii*, and *Meganyctiphanes norvegica* in a Subarctic Fjord, North Norway

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Falk-Petersen, S. 1985. Growth of the euphausiids *Thysanoessa inermis*, *Thysanoessa raschii*, and *Meganyctiphanes norvegica* in a subarctic fjord, North Norway. Can. J. Fish. Aquat. Sci. 42: 14–22.

Growth was studied in terms of the mean carapace length, wet and dry weight, protein, and lipid. Monthly length–weight regressions are presented for a 12-mo period. The growth of *Thysanoessa* spp. is closely related to phytoplankton production, while *Meganyctiphanes norvegica* (a carnivore) increases its weight continuously until it reaches its final size. In I-group *Thysanoessa* the individual maintains its body weight until midwinter, and this is followed by a continuous decrease in the body constituents until the onset of the spring phytoplankton bloom. The growth patterns are correlated with the environmental factors.

Nous avons étudié la croissance de divers Euphasiacés d'après la longueur de la carapace, le poids à l'état frais et à l'état sec et la teneur en protéines et en lipides. Nous avons préparé des courbes de régression représentant le poids en fonction de la longueur mesurés chaque mois pendant 12 mo. La croissance des *Thysanoessa* est étroitement liée à la productivité du phytoplancton ; *Meganyctiphanes norvegica* (espèce carnivore) grossit continuellement jusqu'à ce qu'il atteigne sa taille finale. Le poids des sujets du groupe I (*Thysanoessa*) demeure stable jusqu'au milieu de l'hiver, puis les diverses composantes de l'organisme s'amenuisent graduellement, jusqu'à ce que le phytoplancton commence à proliférer au printemps. Le mode de croissance est lié aux divers facteurs du milieu.

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Euphausiids (krill) have a fundamental role in the marine food chain in high latitudes (Mauchline and Fisher 1969) and represent a key link between phytoplankton production and fish in the fjord food web in North Norway (Falk Petersen and Hopkins 1981a; Falk-Petersen et al. 1981). Euphausiids are found in large quantities as swarms in North Norwegian fjords (Evans and Hopkins 1981), and it is likely that interest will be shown for a commercial fishery in the future.

The assessment and management of euphausiid stocks will depend on analytical models which require information about population structure, recruitment, growth, mortality, and biomass. Solution to the problem of estimating the stock size seems to lie in applying length–weight relationships to population data obtained from preserved material from net-hauls in combination with numerical data obtained by acoustical backscattering models (Å. Kristensen and S. Falk-Petersen, unpubl. data).

Growth is a process of change in mass of a developing individual organism (Winberg 1971; Brett 1979); however, in ecological studies, growth is often expressed as the change in the mean length of a year-class (cohort). To better understand growth patterns and metabolic processes involved in growth it is of interest to express growth of a year-class as wet weight, dry weight, protein, and lipid. The relationship between length and weight must therefore be clarified (Le Cren 1951).

The length ($L$) – weight ($W$) relationship for an organism can be expressed by an equation of the type

$$W = aL^b$$

where $a$ and $b$ are the regression constant and coefficient, respectively (Sokal and Rohlf 1969). Where the body geometry or density of an organism is not changed during growth, the regression coefficient $b = 3$ (isometric growth). If during growth, the length measurement to weight decreases, $b > 3$, and in the opposite case, $b < 3$ (Winberg 1971). Changes in the regression coefficients during life may reflect both physiological processes as well as the influence of the environment (Le Cren 1951; Parker and Larkin 1959).

This paper describes growth in terms of wet weight, dry weight, protein, and lipid for *Thysanoessa inermis*, *Thysanoessa raschii*, and *Meganyctiphanes norvegica* between May 1976 and July 1977. Monthly length–weight regressions for wet weight, dry weight, protein, and lipid against length are presented, and the variation in wet weight, dry weight, protein, and lipid is discussed.

## Materials and Methods

### Zooplankton Sampling

The sampling station was located near Svartnes (69°21′N; 19°06′E) in Balsfjorden where the depth is 180–190 m. The study area, topography, and aspects of the physical environment are given in Eilertsen et al. (1981).

An individual is defined as belonging to 0-group from hatching date to 31 March the following year and considered to change year-class at this date each year. The various year-

TABLE 1. Linear regressions between weight ($W$) and carapace length ($L$) ($\log W = \log a + b (\log L)$ for *T. inermis*. Hypothesis: the regression could not explain a significant part of the variation between length and weight. +, hypothesis accepted; −, hypothesis rejected ($p < 0.05$). $n$ = numbers, $b$ = regression coefficient, $a$ = regression constant.

| Date | Weight weight | | | | Dry weight | | | | Protein | | | | Lipid | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $n$ | $b$ | $a$ | +/− | $n$ | $b$ | $a$ | +/− | $n$ | $b$ | $a$ | +/− | $n$ | $b$ | $a$ | +/− |
| May 1976 | 49 | 2.2031 | 1.202 | − | 46 | 2.3389 | 0.134 | − | | | | | | | | |
| June 1976 | 5 | 4.2908 | 0.015 | − | 5 | 5.0033 | 0.001 | − | | | | | | | | |
| July 1976 | 44 | 2.6372 | 0.533 | − | 43 | 3.0659 | 0.071 | − | 13 | 1.3278 | 0.903 | − | 11 | 1.2229 | 1.381 | + |
| Aug. 1976 | 30 | 2.5430 | 0.682 | − | 31 | 2.8859 | 0.084 | − | 7 | 2.7232 | 0.520 | − | 7 | 2.2900 | 0.173 | − |
| Sept. 1976 | 46 | 2.4707 | 0.820 | − | 45 | 3.1224 | 0.074 | − | 14 | 1.9867 | 0.227 | − | 13 | 2.3443 | 0.161 | − |
| Oct. 1976 | 104 | 2.5887 | 0.636 | − | 103 | 3.0257 | 0.089 | − | 25 | 2.3843 | 0.100 | − | 22 | 3.0475 | 0.042 | − |
| Nov. 1976 | 54 | 2.5323 | 0.746 | − | 54 | 3.0078 | 0.094 | − | 12 | 2.6738 | 0.052 | − | 9 | 3.5296 | 0.018 | − |
| Dec. 1976 | 18 | 2.5264 | 0.712 | − | 17 | 2.9141 | 0.104 | − | | | | | | | | |
| Jan. 1977 | 50 | 2.5799 | 0.704 | − | 50 | 2.9820 | 0.091 | − | 15 | 2.2541 | 0.126 | − | 8 | 2.9864 | 0.045 | − |
| Feb. 1977 | 45 | 2.6077 | 0.657 | − | 45 | 3.1307 | 0.065 | − | 13 | 2.5384 | 0.069 | − | 8 | 1.2934 | 1.096 | + |
| Mar. 1977 | 76 | 2.6408 | 0.641 | − | 72 | 3.0067 | 0.076 | − | 22 | 2.4293 | 0.058 | − | 7 | 1.7622 | 0.339 | + |
| Apr. 1977 | 57 | 2.5883 | 0.746 | − | 55 | 2.9991 | 0.081 | − | 9 | 1.8855 | 0.202 | + | 8 | 0.7731 | 1.587 | + |
| May 1977 | 61 | 2.5313 | 0.764 | − | 57 | 3.0692 | 0.068 | − | 6 | 1.9018 | 0.287 | + | 6 | 1.9809 | 0.246 | − |
| June 1977 | 44 | 2.5648 | 0.695 | − | 43 | 3.1006 | 0.066 | − | 10 | 3.2478 | 0.016 | − | 11 | 3.8499 | 0.007 | − |
| July 1977 | 11 | 3.1682 | 0.210 | − | 11 | 3.4132 | 0.039 | − | 6 | 2.5538 | 0.067 | − | 6 | 3.9388 | 0.006 | − |

TABLE 2. Linear regressions between weight ($W$) and carapace length ($L$) ($\log W = \log a + b (\log L)$ for *T. raschii*. Hypothesis: the regression could not explain a significant part of the variation between length and weight. +, hypothesis accepted; −, hypothesis rejected ($p < 0.05$). $n$ = numbers, $b$ = regression coefficient, $a$ = regression constant.

| Date | Weight weight | | | | Dry weight | | | | Protein | | | | Lipid | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $n$ | $b$ | $a$ | +/− | $n$ | $b$ | $a$ | +/− | $n$ | $b$ | $a$ | +/− | $n$ | $b$ | $a$ | +/− |
| May 1976 | 48 | 2.6679 | 0.521 | − | 41 | 3.2357 | 0.039 | − | | | | | | | | |
| June 1976 | 17 | 2.2420 | 0.993 | − | 15 | 3.3384 | 0.037 | − | 7 | 2.9820 | 0.030 | − | 8 | 4.2856 | 0.003 | − |
| July 1976 | 65 | 2.5179 | 0.753 | − | 64 | 2.9087 | 0.096 | − | 24 | 2.3315 | 0.121 | − | 19 | 1.7071 | 0.298 | − |
| Aug. 1976 | 36 | 2.6549 | 0.634 | − | 36 | 2.6664 | 0.142 | − | 7 | 2.3037 | 0.132 | − | 7 | 1.9459 | 0.233 | + |
| Sept. 1976 | 67 | 2.9757 | 0.367 | − | 67 | 3.4472 | 0.042 | − | 15 | 3.1875 | 0.255 | − | 13 | 4.0772 | 0.005 | − |
| Oct. 1976 | 120 | 2.8836 | 0.417 | − | 121 | 3.3618 | 0.050 | − | 23 | 1.4638 | 0.034 | − | 20 | 2.1286 | 0.157 | − |
| Nov. 1976 | 21 | 2.9176 | 0.409 | − | 21 | 3.2655 | 0.056 | − | 8 | 2.8710 | 0.046 | − | 6 | 0.3524 | 0.210 | + |
| Dec. 1976 | 83 | 3.0565 | 0.327 | − | 78 | 3.3794 | 0.047 | − | 9 | 2.9380 | 0.039 | − | 9 | 3.1510 | 0.032 | − |
| Jan. 1977 | 79 | 2.8952 | 0.431 | − | 78 | 3.1158 | 0.065 | − | 11 | 2.6090 | 0.074 | − | 9 | 3.0146 | 0.006 | − |
| Feb. 1977 | 48 | 2.8582 | 0.449 | − | 47 | 3.2080 | 0.054 | − | 9 | 1.8944 | 0.229 | − | 7 | 1.7146 | 0.314 | + |
| Mar. 1977 | 55 | 2.8340 | 0.496 | − | 56 | 2.9684 | 0.077 | − | 15 | 1.8751 | 0.236 | − | 5 | 1.5891 | 0.346 | − |
| Apr. 1977 | 37 | 2.9947 | 0.388 | − | 36 | 3.0222 | 0.075 | − | | | | | | | | |
| May 1977 | 98 | 2.6269 | 0.645 | − | 98 | 3.0950 | 0.068 | − | 9 | 4.5126 | 0.003 | − | 5 | 2.3212 | 0.097 | − |
| June 1977 | 101 | 2.8476 | 0.459 | − | 98 | 2.8940 | 0.095 | − | 10 | 2.8634 | 0.038 | − | 7 | 0.5559 | 10.130 | + |
| July 1977 | 15 | 2.7519 | 0.469 | − | 14 | 3.2728 | 0.064 | − | 7 | 2.3697 | 0.095 | − | 7 | 0.2398 | 1.931 | + |

classes were separated on the basis of length–frequency with the help of a probability paper.

It was too time consuming to routinely separate the smallest larvae of *T. raschii* and *T. inermis* (see Drobysheva 1957; Berkes 1976). Therefore, a small subsample of 0-group was separated to species each month. There was no significant difference in the mean carapace length of 0-group *T. inermis* and *T. raschii* between May 1976 and March 1977. A common carapace length was therefore calculated for the whole sample of 0-group *Thysanoessa* for this period.

A midwater trawl (mouth 0.7 $m^2$, mesh 1 mm) was used to collect fresh animals for weight measurements. Population data for *Thysanoessa* were collected with two types of Bongo-nets (mouth 0.2 $m^2$, mesh 200 μm; mouth 0.5 $m^2$, mesh 500 μm). The population dynamics of *M. norvegica* are based on material from the midwater trawl. This investigation is based on 60 oblique hauls (from 175 m to the surface) collected on 30-d cruises from May 1976 to July 1977. Further details of zooplankton sampling and the biochemical analyses are given in Falk-Petersen (1981) and Falk-Petersen and Hopkins (1981b).

## Data Analyses

Length–weight (wet weight, dry weight, protein, and lipid) data were analysed using the allometric equation

$$W = aL^b$$

$$\log W = \log a + b (\log L)$$

where $W$ = weight and $L$ = carapace length. Each regression was first tested (Student's $t$-test, confidence limits $p = 0.05$) to see if the regression coefficient could explain a significant part of the variation between weight and length. The monthly regression lines were then compared by analyses of covariance to test ($F$-test, $p = 0.05$) whether the regression coefficients

TABLE 3. Linear regressions between weight ($W$) and carapace length ($L$) ($\log W = \log a + b(\log L)$ for *M. norvegica*. Hypothesis: the regression could not explain a significant part of the variation between length and weight. +, hypothesis accepted; −, hypothesis rejected ($p \leq 0.05$). $n$ = numbers, $b$ = regression coefficient, $a$ = regression constant.

| | Weight weight | | | | Dry weight | | | | Protein | | | | Lipid | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | $n$ | $b$ | $a$ | +/− | $n$ | $b$ | $a$ | +/− | $n$ | $b$ | $a$ | +/− | $n$ | $b$ | $a$ | +/− |
| May 1976 | 15 | 3.3107 | 0.1512 | − | 15 | 3.0245 | 0.0668 | − | | | | | | | | |
| June 1976 | 14 | 2.8215 | 0.4796 | − | 14 | 2.8325 | 0.1089 | − | 5 | 2.4555 | 0.1208 | + | 6 | 4.4424 | 0.0005 | + |
| July 1976 | 31 | 2.7141 | 0.6982 | − | 31 | 2.8101 | 0.1401 | − | 15 | 2.5593 | 0.0997 | − | 11 | 3.0426 | 0.0265 | − |
| Sept. 1976 | 12 | 2.8229 | 0.6063 | − | 12 | 2.5748 | 0.2929 | − | | | | | | | | |
| Oct. 1976 | 8 | 2.6236 | 0.9307 | − | 8 | 2.9309 | 0.1299 | − | 7 | 1.3434 | 2.4740 | + | 6 | 2.8350 | 0.0722 | − |
| Nov. 1976 | 8 | 2.7114 | 0.7449 | − | 8 | 2.8013 | 0.1693 | − | 6 | 2.5742 | 0.1217 | − | 6 | 2.6971 | 0.0823 | − |
| Jan. 1977 | 33 | 2.6931 | 0.7797 | − | 32 | 3.0218 | 0.0966 | − | 15 | 2.6427 | 0.0837 | − | 10 | 2.9712 | 0.0424 | − |
| Feb. 1977 | 16 | 2.7391 | 0.8257 | − | 16 | 2.8991 | 0.1126 | − | 7 | 2.3526 | 0.1485 | − | 5 | 3.1371 | 0.0245 | − |
| Mar. 1977 | 18 | 2.8157 | 0.5731 | − | 18 | 1.1702 | 0.0612 | − | 6 | 2.5556 | 0.0839 | − | 6 | 3.1544 | 0.0250 | − |
| Apr. 1977 | 29 | 3.0907 | 0.3703 | − | 28 | 3.3342 | 0.0476 | − | 7 | 3.3639 | 0.0101 | − | 5 | 4.8552 | 0.0004 | + |
| May 1977 | 28 | 2.7782 | 0.7372 | − | 24 | 2.9554 | 0.1181 | − | 8 | 2.5420 | 0.1292 | − | 7 | 2.0942 | 0.2695 | − |
| June 1977 | 32 | 2.8263 | 0.6477 | − | 31 | 3.1685 | 0.0694 | − | 9 | 2.6215 | 0.0980 | − | 7 | 3.5525 | 0.0096 | − |
| July 1977 | 9 | 2.9906 | 0.4213 | − | 9 | 3.1898 | 0.0658 | − | 6 | 3.4947 | 0.0123 | − | 5 | 3.0479 | 0.0278 | − |

TABLE 4. Comparison of the monthly regression line (ANOVA) for *T. inermis*, *T. raschii*, and *M. norvegica*. Hypothesis: HoI, the regression coefficients are similar; HoII, the regression constants are similar; +, hypothesis accepted; −, hypothesis rejected. $b$ = regression coefficient, $a$ = regression constant.

| Species | Independent variable | Dependent variable | Estimated $F$-values: Between $b$ | Estimated $F$-values: Between $a$ | Degrees of freedom: $df_1$ | Degrees of freedom: $df_2$ | HoI | HoII |
|---|---|---|---|---|---|---|---|---|
| *T. inermis* | Carapace length (mm) | Wet weight (mg) | 5.810 | 15.244 | 14 | 678 | − | − |
| | | Dry weight (mg) | 4.719 | 66.402 | 14 | 661 | − | − |
| | | Protein (mg) | 1.267 | 2.953 | 11 | 139 | + | − |
| | | Lipid (mg) | 2.975 | 7.360 | 11 | 103 | − | − |
| *T. raschii* | Carapace length (mm) | Wet weight (mg) | 6.988 | 11.125 | 14 | 878 | − | − |
| | | Dry weight (mg) | 8.521 | 16.901 | 14 | 854 | − | − |
| | | Protein (mg) | 3.707 | 7.806 | 12 | 140 | − | − |
| | | Lipid (mg) | 3.632 | 7.353 | 12 | 108 | − | − |
| *M. norvegica* | Carapace length (mm) | Wet weight (mg) | 2.730 | 23.243 | 12 | 239 | − | − |
| | | Dry weight (mg) | 1.724 | 14.634 | 12 | 232 | + | − |
| | | Protein (mg) | 2.745 | 10.745 | 10 | 79 | − | − |
| | | Lipid (mg) | 1.412 | 8.533 | 10 | 62 | + | − |

were significantly different and, if not, whether the regression constants were significantly different. When there was no significant difference between the regression coefficients, a common regression coefficient was calculated, which was then used to recalculate the regression constant (see Sokal and Rohlf 1969).

### Growth Concepts

The estimated growth of a year-class is normally based on changes in the length–frequency distribution within a year-class (age-group) and often expressed as the change in the mean length and the relevant confidence limits with time. The time-related change of the length–frequency distribution is dependent on both the growth of the individual animals and external factors such as selective mortality and/or sampling errors. The mean growth in terms of weights was estimated from monthly means of carapace length based on length–weight regressions.

The concept of "standard" animals has been used by several authors to eliminate size (length) as a variable (Båmstedt 1976). By calculating the weight of a theoretical animal with a fixed length from length–weight regressions, length is reduced, if not totally eliminated, as a variable, and the weight of animals of the same length but from different periods can be compared. The variation in weight so obtained is referred to as growth of a standard individual in this paper.

## Results

### Weight–Length Relationships

*Thysanoessa inermis*

There were significant relationships between wet weight, dry weight, and length in all months. Protein and length were significantly related in all months except April and May 1977, as were lipid and length in all months except July 1976 and February, March, and April 1977 (Table 1). Regressions of wet weight, dry weight, and lipid on length were different (ANOVA) between months. The corresponding coefficients obtained for

TABLE 5. Regression analyses for weight against carapace length for *T. inermis* and *M. norvegica*. Data of tables 1 and 3 recalculated for a common regression coefficient (*b*). *a* = regression constant, SD = standard deviation.

| | | | | | *M. norvegica* | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *T. inermis*, protein | | | | Dry weight | | | | Protein | | | |
| Date | *b* | SD | *a* | SD | *b* | SD | *a* | SD | *b* | SD | *a* | SD |
| May 1976 | | | | | 3.028 | 0.039 | 0.066 | 0.076 | | | | |
| June 1976 | | | | | 3.028 | 0.039 | 0.069 | 0.075 | 2.924 | 0.119 | 0.021 | 0.17 |
| July 1976 | 2.387 | 0.082 | 0.098 | 0.109 | 3.028 | 0.039 | 0.083 | 0.076 | 2.924 | 0.119 | 0.035 | 0.17 |
| Aug. 1976 | 2.387 | 0.082 | 0.100 | 0.107 | | | | | | | | |
| Sept. 1976 | 2.387 | 0.082 | 0.102 | 0.108 | 3.028 | 0.039 | 0.096 | 0.076 | | | | |
| Oct. 1976 | 2.387 | 0.082 | 0.099 | 0.107 | 3.028 | 0.039 | 0.103 | 0.075 | 2.924 | 0.119 | 0.058 | 0.17 |
| Nov. 1976 | 2.387 | 0.082 | 0.091 | 0.106 | 3.028 | 0.039 | 0.101 | 0.074 | 2.924 | 0.119 | 0.049 | 0.16 |
| Jan. 1977 | 2.387 | 0.082 | 0.099 | 0.104 | 3.028 | 0.039 | 0.095 | 0.075 | 2.924 | 0.119 | 0.048 | 0.16 |
| Feb. 1977 | 2.387 | 0.082 | 0.091 | 0.104 | 3.028 | 0.039 | 0.083 | 0.075 | 2.924 | 0.119 | 0.040 | 0.16 |
| Mar. 1977 | 2.387 | 0.082 | 0.090 | 0.098 | 3.028 | 0.039 | 0.084 | 0.071 | 2.924 | 0.119 | 0.042 | 0.16 |
| Apr. 1977 | 2.387 | 0.082 | 0.082 | 0.104 | 3.028 | 0.039 | 0.097 | 0.075 | 2.924 | 0.119 | 0.050 | 0.17 |
| May 1977 | 2.387 | 0.082 | 0.114 | 0.105 | 3.028 | 0.039 | 0.100 | 0.075 | 2.924 | 0.119 | 0.039 | 0.168 |
| June 1977 | 2.387 | 0.082 | 0.086 | 0.107 | 3.028 | 0.039 | 0.096 | 0.07 | 2.924 | 0.119 | 0.040 | 0.166 |
| July 1977 | 2.387 | 0.082 | 0.093 | 0.106 | 3.028 | 0.039 | 0.095 | 0.075 | 2.924 | 0.119 | 0.037 | 0.170 |

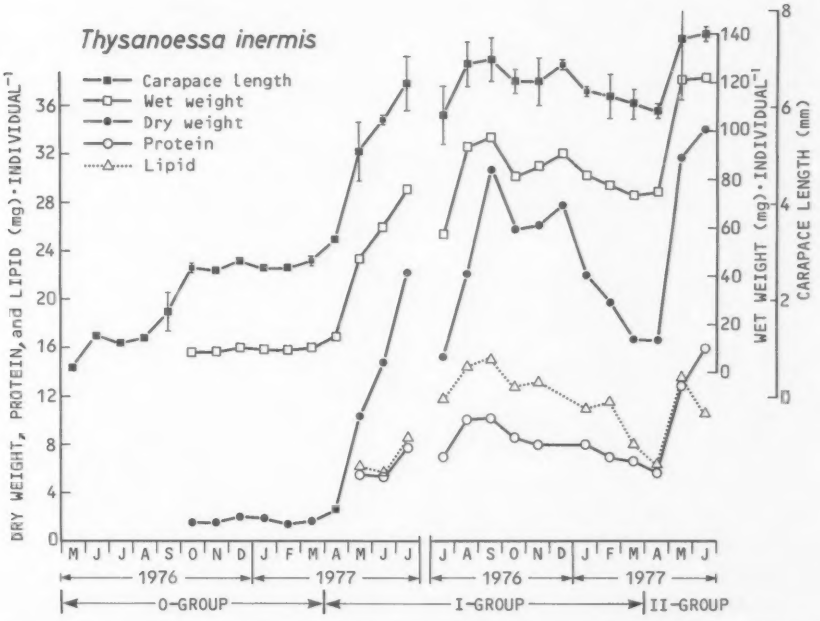


FIG. 1. Mean growth of year-classes in terms of carapace length, wet weight, dry weight, protein, and lipid for *T. inermis* (Balsfjorden, North Norway). The variation in weights are calculated from the mean carapace length. The axes are broken between I-group from 1976 and I-group from 1977.

the regression of protein on length did not differ significantly from each other (see Table 4). A common regression coefficient and constant were therefore determined for the 12 mo (see Table 5).

The regression coefficient (*b*) for wet weight was less than 3 (2.2–2.65) for all months except for June 1976 and July 1977; for dry weight, *b* averaged approximately 3 (2.8–3.4) except for May and June 1976; for protein the common regression coefficient *b* was 2.39, while for lipid, *b* varied between 2 and 4 for those regressions that were significant (Table 1). This indicates that wet weight and protein decreased, while dry weight did not change relative to length increases. There were no clear trends for lipid.

*Thysanoessa raschii*

There were significant relationships between wet weight, dry weight, and protein against length for all months. Lipid and length were significantly related in all months except for August and November 1976 and February, June, and July 1977 (Table 2). The regression coefficients obtained for the regressions of

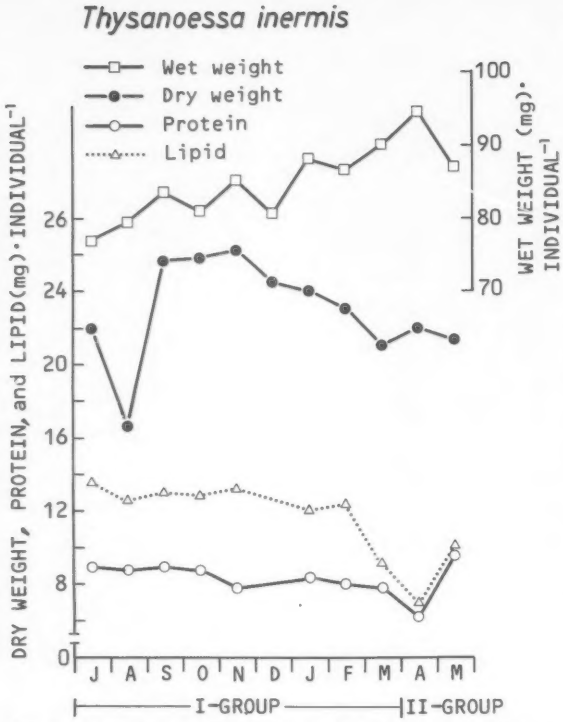


FIG. 2. Growth of a standard individual in terms of wet weight, dry weight, protein, and lipid for *T. inermis* (Balsfjorden, North Norway). The variation in weights are estimated for a theoretical animal of 6.5-mm carapace length.

wet weight, dry weight, protein, and lipid on length were different (ANOVA) between months (see Table 4).

The regression coefficient (*b*) for wet weight was less than 3 (2.24–2.99) for all months except December 1976; for dry weight, *b* averaged approximately 3 (2.89–3.45); for protein, *b* was less than 3 (1.88–2.98) for all months except September 1976 and May 1977, while for lipid, *b* varied between 1.71 and 4.28 for those regressions that were significant. *Thysanoessa raschii* thus showed similar trends to *T. inermis*.

*Meganyctiphanes norvegica*

There was a significant relationship between wet weight and dry weight against length for all months. Protein and length were significantly related for all months except June and October 1976, as were lipid weight and length in all months except for June 1976 and April 1977 (Table 3). The regression coefficients obtained for the regression of wet weight and lipid weight on length were different (ANOVA) between months. The corresponding coefficients obtained for the regression of dry weight on length and protein on length did not differ significantly (Table 4), and a common regression coefficient and constant were therefore determined (Table 5).

The regression coefficient (*b*) for wet weight was less than 3 (2.62–2.99) for all months except for May 1976 and April 1977; for dry weight the common regression coefficient *b* was 3.03; for protein, *b* was 2.92, while for lipid, *b* varied between 2.09 and 3.55 for the significant regressions. This indicates that wet weight and protein decreased relative to length increases, while dry weight did not change.

## Estimated Growth

*Thysanoessa inermis*

No growth could be seen during winter for 0-group (Fig. 1). In I-group there is a rapid growth from April until August–

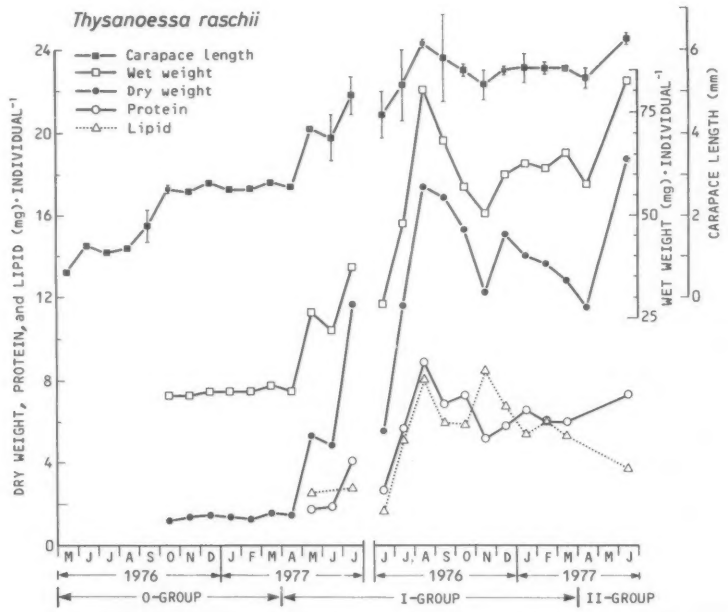


FIG. 3. Mean growth of year-classes in terms of carapace length, wet weight, dry weight, protein, and lipid for *T. raschii* (Balsfjorden, North Norway). The variation in weights are calculated from the mean carapace length. The axes are broken between I-group from 1976 and I-group from 1977.

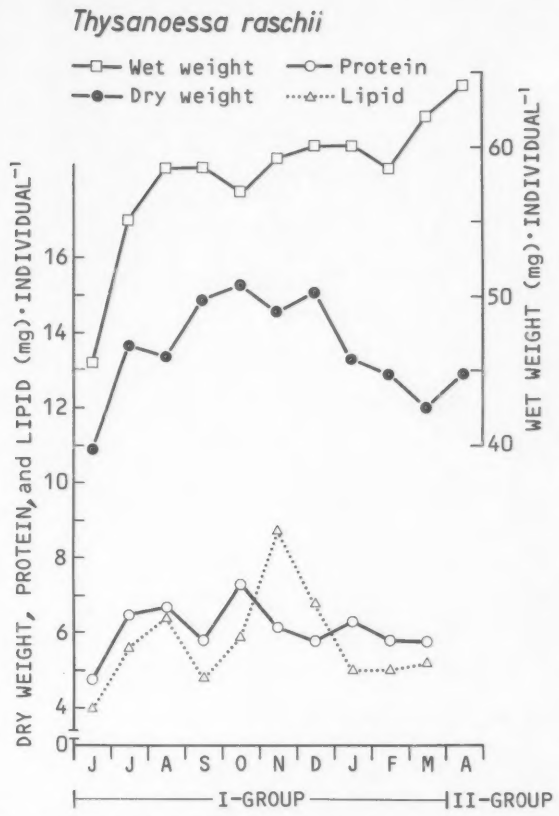


FIG. 4. Growth of a standard individual in terms of wet weight, dry weight, protein, and lipid for *T. raschii* (Balsfjorden, North Norway). The variation in weights are estimated for a theoretical animal of 5.5-mm carapace length.

September. Wet weight increased 9.5-fold (10–95 mg) and dry weight 11-fold (2–22 mg). During winter, I-group decreased in weight, which is partly associated with a decrease in length. From August–September until April both dry weight (31–16 mg) and protein (10–5 mg) halved, lipid decreased 2.5-fold (15–6 mg), while wet weight decreased only slightly (95–75 mg).

Growth was calculated for a theoretical animal of 6.5-mm carapace length. Animals of this length were present in the sampled population from July 1976 until May 1977. The standard individual belonging to I-group increased in wet weight and dry weight from July until November (Fig. 2). Wet weight continued to increase until April (max. approximately 95 mg), while there was a considerable decrease in dry weight (26–21 mg) from November until March. Protein decreased (9–6 mg) slightly from July through to April, while lipid decreased slowly from July to February before a pronounced decrease (12–7 mg) occurred between February and April. It is interesting to note that wet weight decreased from April to May in II-group, while protein and lipid increased.

*Thysanoessa raschii*

No growth could be seen during winter in 0-group (Fig. 3). In I-group the growth period lasted from April to August, with wet weight increasing 10.5-fold (7.5–80 mg) and dry weight increasing 11.5-fold (1.5–17.5 mg). There was a considerable decrease in wet weight (80–50 mg), dry weight (17–12 mg), and protein (9–5 mg) in the autumn, from August to November. Lipid decreased from August to September–October, increased again, and reached its highest level (8.5 mg) in November. During winter, I-group increased in wet weight until March, while dry weight and lipid, after an increase in November–December, decreased until the following spring.

Growth was calculated for a theoretical animal of 5.5-mm carapace length. Animals of this length were present in the sampled population between June 1976 and May 1977. The standard individual belonging to I-group increased relatively rapidly in wet weight (45–58 mg), dry weight (11–13 mg), protein (6–6.5 mg), and lipid (4–6.5 mg) from June until August (Fig. 4). Wet weight continued to increase until a maximum (63 mg) was reached in April, while dry weight reached a maximum in September–October (15 mg) and then decreased continuously until April (12 mg). Protein was relatively stable (approximately 6 mg) from September until May, while lipid increased greatly from September to November (5–8.5 mg) before stabilizing at approximately 5 mg between January and May. In the standard individual from the II-group, wet weight decreased after March–April, while dry weight increased.

*Meganyctiphanes norvegica*

Because of uncertain population structure (see Falk-Petersen and Hopkins 1981b) reliable estimates of growth could be calculated only between January and July both in 1976 and 1977. In 0- and I-group a slow and continuous growth took place during winter and spring until July (Fig. 5). In I- and II-group wet weight was relatively stable (approximately 700 mg) from January until March. Dry weight (185–160 mg) and protein (65–35 mg) decreased from January until April, while lipid (63–52 mg) decreased until June. Both dry weight and protein increased from March until April.

Growth was calculated for a theoretical animal of 12-mm carapace length. Animals of this length were present in the sampled population from January until July 1977. In individuals belonging to I- and II-group wet weight (approximately 600 mg) was relatively stable from January to March until increasing to a marked maximum (800 mg) in April (Fig. 6). Dry weight decreased (175–155 mg) from January until February before increasing to 180 mg in May. Protein decreased continuously (60–40 mg) from January until April before a marked increase to 70 mg occurred in May. Lipid peaked (70 mg) in April before decreasing until May.

## Discussion

The population dynamics, the seasonal variation in weight, protein, lipid, lipid classes, and fatty acids for *T. inermis*, *T. raschii*, and *M. norvegica* have been outlined earlier (Falk-Petersen and Hopkins 1981b; Falk-Petersen 1981; Falk-Petersen et al. 1981; Sargent and Falk-Petersen 1981). In this paper some of the growth parameters are presented, and differences between growth patterns of individual animals and the population (year-classes) are discussed with reference to the environment. The growth of *T. inermis* and *T. raschii* starts in April and is closely related to phytoplankton production. It is interesting to note that although 0-group *T. inermis* and *T. raschii* have similar lengths during winter, the dry weight of *T. inermis* (16 mg) is double that of *T. raschii* (8 mg). There is a rapid growth with a 10-fold increase in wet weight and an 11-fold

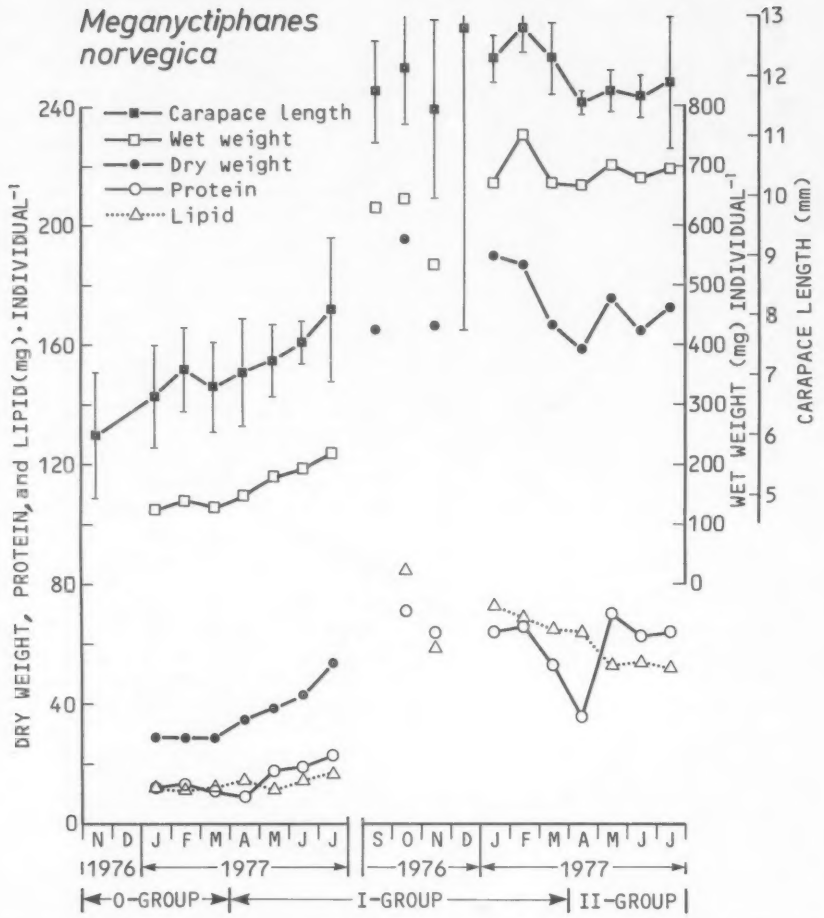


FIG. 5. Mean growth of year-classes in terms of carapace length, wet weight, dry weight, protein, and lipid for *M. norvegica* (Balsfjorden, North Norway). The variation in weights are calculated from the mean carapace length. The axes are broken between I-group from 1976 and I-group from 1977.

increase in dry weight for I-group *Thysanoessa* in 4–5 mo. In this period the temperature varied between 2 and 5°C, and in the most active growth phase in May the temperature was approximately 2°C. The rapid growth shows that the animals must have a highly efficient biosynthesis despite the low sea temperature. Henderson et al. (1981, 1982) also showed that fatty acid biosynthesis of *T. inermis* from the coldwater Balsfjorden (70°N) was more than triple that of *T. raschii* from the temperate Clyde Estuary, Scotland (55°N). This supports the conclusion of Clarke (1980) that the constraints leading to an overall reduced growth in high latitudes are not physico–chemical, but ecological.

The measured growth of a year-class may differ from that of an individual animal if the growth of the population as such does not reflect events in individual animals, but is due to external factors such as selective mortality or sampling errors (Ricker 1975). To get a theoretical expression for the growth of individuals the term standard individual is used.

In I-group *T. inermis* there is an overall decrease in both the mean carapace length and weight during autumn and winter. The same trend is apparent for *T. raschii* except that there is a marked decrease in autumn followed by a slightly higher but stable level in both carapace length and wet weight during midwinter. The wet weight of a standard individual does, however, increase markedly during this period, indicating that the individual animal increases the amount of water in the body during winter. During autumn there is a marked decrease in the mean dry weight in I-group *T. raschii*. This does not, however, reflect events in the animals themselves, since there is an increase in dry weight in individual animals. The same trend can be seen in *T. inermis*. There are strong indications that the increase in lipid seen in November–December in individual *T. raschii* is due to dietary input of phytol (Sargent and Falk-Petersen 1981). Falk-Petersen et al. (1981) postulated that growth could continue, especially for *T. raschii*, until December on benthic detritus or on the relatively abundant nonliving particles suspended in the water column during winter. In I-group *T. inermis* there is a pronounced decrease in the mean carapace length as well as in the dry weight of the standard individual from December to April. The decrease in the mean dry weight of the I-group *T. inermis* from December to April can therefore be explained by a decrease in the mean length of the

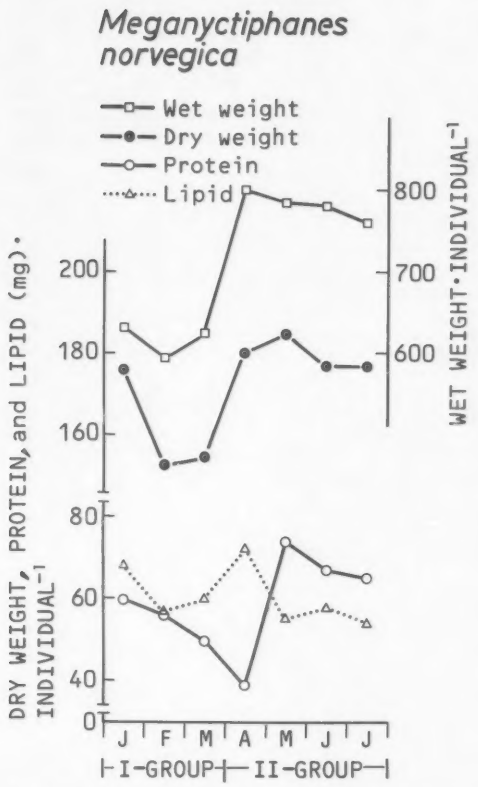


FIG. 6. Growth of a standard individual in terms of wet weight, dry weight, protein, and lipid for *M. norvegica* (Balsfjorden, North Norway). The variation in weights are estimated for a theoretical animal of 12-mm carapace length.

age-group as well as a decrease in dry weight of individual animals. In the same period, the mean carapace length of I-group *T. raschii* is stable, while the dry weight of the standard individual decreases. The decrease in the mean dry weight in I-group *T. raschii* from December to April therefore reflects events in the individual animals.

For *T. inermis* and *T. raschii* the decrease in dry weight, protein, and lipid for the standard animal is first seen in November–December and lasts through to March. This indicates that a negative energy balance (starvation) lasts from midwinter until the onset of the primary production, probably due to a lack of adequate food to meet the energy required for (1) maintenance of basal metabolism during overwintering and (2) gonad formation (Falk-Petersen et al. 1981).

In standard individuals of I-group euphausiids from Balsfjorden, there was a decrease in dry weight and an increase in wet weight during the last part of the winter. The reverse situation occurred in spring with an increase in dry weight and decrease in wet weight. The regulation of the water content enables the individual animal to keep the body form both in periods of starvation and high food intake. This capability might have both metabolic and physiological advantages. Omori (1969) and Raymont et al. (1971) also showed that a decrease in dry weight in zooplankton is often compensated for by a increase in the water content. There are also reverse relationships between lipid and wet weight for the standard individual from *T. inermis* and *T. raschii*. This is in agreement with the investigations of Childress and Nygaard (1973, 1974) for zooplankton and small fish.

From the regression coefficient in the length–weight regressions, it is also seen that there is a general tendency for wet weight and protein to decrease, while dry weight does not change relative to length increases.

While the growth patterns of the two *Thysanoessa* spp. are related to the phytoplankton production, *Meganyctiphanes norvegica*, which is a carnivore in Balsfjorden (Sargent and Falk-Petersen 1981), increased its weight continuously until it reached its final size as I-group in January.

In I-group *M. norvegica* there is a decrease in carapace length between January and March, while in summer there are only small changes in carapace length. The wet and dry weight of individual animals do, however, increase markedly between March and April. This probably reflects both (1) an increase in the food quality due to the onset of feeding of the smaller zooplankton on phytoplankton and (2) an increase in food availability due to the spawning of the spring-spawning animals.

There is a decrease in the mean carapace length during winter for I-group *T. inermis*, *T. raschii*, and *M. norvegica* (Falk-Petersen and Hopkins 1981b). This could be caused by factors such as selective mortality or sampling error but could also be due to body shrinkage. This has been demonstrated in *Euphausia superba* in which reduction in body size occurred after a long period of starvation (Ikeda and Dixon 1982).

The arctic environment, with a short period of abundant food followed by long periods of food shortage, places constraints on pelagic animals. It has been suggested that the euphausiids *T. inermis*, *T. raschii*, and *M. norvegica* have different overwintering strategies (Falk-Petersen et al. 1982). *Thysanoessa inermis* stores large amounts of energy as wax esters and triacylglycerols during the summer months, and these are utilised as an energy source during winter. *Thysanoessa raschii* lays down lipids (triacylglycerols) during summer but also has the ability to feed on detritus of plant origin during the winter. On the other hand, *M. norvegica* feeds throughout the winter as a pure carnivore. Nevertheless, the three krill species do show decreases in carapace length during winter. Body shrinkage, as suggested by Ikeda and Dixon (1982), may be a mechanism by which energy requirements could be reduced, increasing the chances of overwinter survival.

## References


BÅMSTEDT, U. 1976. Studies on the deep-water pelagic community of Korsfjorden, western Norway. Changes in the size and biochemical composition of *Meganyctiphanes norvegica* (Euphausiacea) in relation to its life cycle. Sarsia 61: 15–30.

BERKES, F. 1976. Ecology of euphausiids in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 1894–1905.

BRETT, J. R. 1979. Environmental factors and growth, p. 599–675. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. VIII. Academic Press Inc., London.

CHILDRESS, J. J., AND M. H. NYGAARD. 1973. The chemical composition of midwater fishes as a function of depth of occurrence off Southern California. Deep-Sea Res. 20: 1093–1109.

1974. The chemical composition of midwater crustaceans as a function of depth of occurrence off Southern California. Mar. Biol. 27: 225–238.

CLARKE, A. 1980. A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. Biol. J. Linn. Soc. 14: 77–92.

DROBYSHEVA, S. S. 1957. The effect of some aspects of the biology of Euphausiacea upon the summer feeding conditions for cod in the Barents Sea. Tr. Polyarn. Nauchno-Issled. Preoktn. Inst. Morsk. Rybn. Khoz. Okeanogr. 10: 106–124. (Transl. from Russian, Fish Res. Board Can.)

EILERTSEN, H.-CHR., S. FALK-PETERSEN, C. C. E. HOPKINS, AND K. TANDE. 1981. Ecological investigations on the plankton community of Balsfjorden, Northern Norway: the study area, topography and environmental parameters. Sarsia 66: 25–34.

EVANS, R. A., AND C. C. E. HOPKINS. 1981. Zooplankton sound scattering layers in North Norwegian fjords: distribution and biomass in February–March 1978. Sarsia 66: 147–160.

FALK-PETERSEN, S. 1981. Ecological investigations on the zooplankton community of Balsfjorden, Northern Norway: seasonal changes in body weight and the main biochemical composition of *Thysanoessa inermis* (Krøyer), *Thysanoessa raschii* (M.Sars) and *Meganyctiphanes norvegica* (M.Sars) in relation to environmental parameters. J. Exp. Mar. Biol. Ecol. 49: 103–120.

FALK-PETERSEN, S., R. R. GATTEN, C. C. E. HOPKINS, AND J. R. SARGENT. 1981. Ecological investigation on the zooplankton community of Balsfjorden, Northern Norway: seasonal variation in the lipid class composition of the Arctic Boreal krill, *Thysanoessa inermis* (Krøyer), *Thysanoessa raschii* (M.Sars) and *Meganyctiphanes norvegica* (M.Sars). J. Exp. Mar. Biol. Ecol. 54: 209–224.

FALK-PETERSEN, S., AND C. C. E. HOPKINS. 1981a. Zooplankton sound scattering layers in North Norwegian fjords: interactions between fish and krill shoals in a winter situation in Ullsfjorden and Øksfjorden. Proc. 15th Eur. Symp. Mar. Biol. Kieler Meeresforsch, Sondeh. 5: 191–201.

1981b. Ecological investigations on the zooplankton community of Balsfjorden, Northern Norway: population dynamics of the euphausiids *Thysanoessa inermis* (Krøyer), *Thysanoessa raschii* (M.Sars) and *Meganyctiphanes norvegica* (M.Sars) in 1976 and 1977. J. Plankton Res. 3(2): 177–192.

HENDERSON, R. J., S. FALK-PETERSEN, AND J. R. SARGENT. 1982. The composition and biosynthesis of lipids in *Thysanoessa raschii* from the Clyde Estuary, Scotland. Mar. Biol. 70: 7–12.

HENDERSON, R. J., J. R. SARGENT, AND S. FALK-PETERSEN. 1981. Lipogenesis in the Arctic Euphausiid *Thysanoessa inermis*. Mar. Biol. 63: 235–240.

IKEDA, T., AND P. DIXON. 1982. Body shrinkage as a possible overwintering mechanism of the Antarctic krill, *Euphausia superba* Dana. J. Exp. Mar. Biol. Ecol. 62: 143–151.

LE CREN, E. D. 1951. The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. 20: 201–219.

MAUCHLINE, J., AND C. R. FISHER. 1969. The biology of euphausiids, p. 1–454. *In* F. S. Russel and M. Younge [ed.] Advances in marine biology. Vol. 7. Academic Press, London and New York.

OMORI, M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. Mar. Biol. 3: 4–10.

PARKER, R. R., AND P. A. LARKIN. 1959. A concept of growth of fishes. J. Fish. Res. Board Can. 16: 721–745.

RAYMONT, J. E. G., R. T. SRINIVAGASAM, AND J. K. B. RAYMONT. 1971. Biochemical studies on marine zooplankton. VIII. Further investigations on *Meganyctiphanes norvegica* (M.Sars). Deep-Sea Res. 18: 1167–1178.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 1–382.

SARGENT, J. R., AND S. FALK-PETERSEN. 1981. Ecological investigations on the zooplankton community of Balsfjorden, Northern Norway: lipids and fatty acids in *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *Thysanoessa inermis* during midwinter. Mar. Biol. 62: 131–137.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Company, San Francisco, CA. 776 p.

WINBERG, G. G. [ED.] 1971. Methods for the estimation of production of aquatic animals. Academic Press, London and New York. 179 p.

# Accumulation of Copper and Zinc in the Yellow Water Lily, *Nuphar variegatum*: Relationships to Metal Partitioning in the Adjacent Lake Sediments

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Campbell, P. G. C., A. Tessier, M. Bisson, and R. Bougie. 1985. Accumulation of copper and zinc in the yellow water lily, *Nuphar variegatum*: relationships to metal partitioning in the adjacent lake sediments. Can. J. Fish. Aquat. Sci. 42: 23–32.

Relationships between the partitioning of Cu and Zn in lake sediments and their availability to the yellow water lily, *Nuphar variegatum*, were examined downstream from a major Cu/Zn mining and smelting complex in Northwestern Quebec, Canada. At each of 13 sampling sites, five *N. variegatum* individuals were collected, separated into stem and rhizome portions, and analyzed for total Cu and Zn. At the same sites, sediment cores were collected at the base of each plant; the 0- to 2-cm stratum was extruded, wet sieved (850 μm), and subjected to a sequential leaching procedure to determine the partitioning of Cu and Zn among various operationally defined geochemical fractions. Statistical analysis suggested that a significant portion of the Cu burden in *N. variegatum* was probably derived from the sediments, whereas the Zn content of the plant originated largely in the water column. The concentrations of Cu in the fractions most readily extracted from the sediment were the best indicators of Cu bioavailability in the sediment; normalization of these concentrations with respect to the Fe content of the sediment improved the relationship with $[Cu_{rhizome}]$, suggesting that Fe may play a protective role in regulating Cu bioavailability.

Au cours d'une étude menée en aval du complexe minier de Rouyn-Noranda, dans le nord-ouest du Québec, on a examiné les relations entre les répartitions du Cu et du Zn entre différentes phases des sédiments et la biodisponibilité de ces métaux envers *Nuphar variegatum*. À chacun des 13 sites d'échantillonnage, cinq spécimens individuels de *N. variegatum* ont été prélevés, et les tiges et rhizones ont été analysés séparément pour leur contenu en Cu et Zn total. Aux même sites, des carottes de sédiments ont été prélevées au pied de chaque plante ; la strate 0–2 cm était retenue, tamisée par voie humide (850 μm) et soumise à une procédure d'extractions séquentielles pour déterminer la répartition de Cu et Zn entre diverses fractions géochimiques définies opérationnellement. L'analyse statistique suggère qu'une partie significative du Cu contenu dans *N. variegatum* provenait probablement des sédiments, contrairement au Zn, qui semblait provenir largement de la colonne d'eau. Les concentrations de Cu dans les fractions extraites les plus facilement des sédiments étaient les meilleurs indicateurs de la biodisponibilité du Cu dans les sédiments ; la normalisation de ces concentrations par rapport au contenu en Fe des sédiments améliorait les relations avec $[Cu_{rhizome}]$, suggérant que le Fe peut jouer un rôle protecteur en contrôlant la biodisponibilité du Cu.

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Rooted aquatic plants concentrate various metals from their immediate environment; concentration factors as high as $10^3$–$10^4$ have been observed with respect to water (for reviews see Hutchinson 1975; Boyd 1978; Dykyjova 1979). Recent research in this area has evolved in two complementary directions: to quantify the role of macrophytes in the biogeochemical cycling of certain metals, i.e. the mobilization of sediment-bound metals (Lee et al. 1976; Welsh and Denny 1976; McIntosh et al. 1978; Gallagher and Wolf 1980; Larsen and Schierup 1981; Gommes and Muntau 1981b), and to identify certain biomonitor species that would be useful for monitoring metal pollution in the aquatic environment (Adams et al. 1973; Dietz 1973; Hutchinson et al. 1975; Ray and White 1976, 1979; Franzin and McFarlane 1980; Aulio 1980; Miller et al. 1983).

Two pathways exist for the uptake of trace metals in the stems and leaves of freshwater macrophytes: (i) direct uptake from the water column or (ii) uptake from the interstitial water in the sediments followed by acropetal translocation from the roots to the stems and leaves. This same duality of pathways exists for other solutes (e.g. phosphorus), and both accumulation routes may be operative in the same plant (Denny 1980). Factors influencing the uptake of metals by macrophytes include such biological variables as plant anatomy (Welsh and Denny 1979; Franzin and McFarlane 1980), seasonal plant development (Mayes et al. 1977; Mudroch and Capobianco 1978; Ray and White 1979; Larsen and Schierup 1981), and community structure (Auclair 1979; Mudroch and Capobianco 1979). General environmental conditions may also affect metal uptake by macrophytes, notably the ambient water quality (Kinkade and Erdman 1975; Franzin and McFarlane 1980) and the prevailing metal concentrations (Dietz 1973; Hutchinson et al. 1975; Mayes et al. 1977; Harding and Whitton 1978; Mudroch and Capobianco 1978; Aulio 1980; Welsh and Denny 1980).

With particular reference to this latter group of factors, if pathway (ii) were widespread one might expect the concentration of a metal in the sediment substrate to influence the metal concentration in the plant. However, a literature review covering some 105 cases where metal concentrations had been determined both in the plants and in the underlying sediments revealed that fully 65% of the cases showed no relationships between these two parameters; in an additional 5% of the cases, a negative correlation existed between the metal content of the plant, $[M_p]$, and that of the sediments, $[M_{sed}]$. A possible explanation for this apparent independence of $[M_{sed}]$ and $[M_p]$, besides the obvious one that metal uptake directly from the water column masks sediment–plant relationships, is that past workers in this area have largely ignored the partitioning of the metals associated with the sediments, i.e. their distribution among various particulate phases. The partitioning of sediment-bound metals influences their bioavailability to a number of benthic invertebrates (Jenne and Luoma 1977; Luoma and Bryan 1978, 1979; Langston 1982) and one might anticipate that a similar situation would prevail for rooted macrophytes.

The purpose of the present study was to examine relationships between the partitioning of copper and zinc in lake sediments and the concentrations of these metals in aquatic plants in the field.

## Study Area

To meet the study objective, the ideal field site would encompass a spatial gradient in metal concentrations in the sediments, $[M_{sed}]$, but not in the overlying water column. Such a situation would be approached downstream from a former source of metal pollution, now controlled; metal concentrations in the circumneutral water column would be reduced close to background levels, but those in the sediments would still exhibit a marked downstream gradient. The chosen study area, which approximated this ideal situation, is located in northwestern Quebec some 500 km northwest of Montreal, near Rouyn–Noranda (Fig. 1). In this region, the bedrock is covered by locally derived glacial till and, at the surface, by lacustrine clays deposited during the existence of the proglacial lake Barlow–Ojibway (Lalonde and Lasalle 1983). This unconsolidated material, generally 15–20 m deep, is underlain by various lithological units, some of which contain important Cu and Zn deposits and have been extensively exploited. Many metal anomalies are observed in the lacustrine clays; additional sources of metal contamination in the area include abandoned mines, current mining operations, accumulated residues from the smelting process, and atmospheric fallout from the smelter emissions. The mining operations are scattered throughout the study area, but the smelters and waste disposal activities are located in the immediate vicinity of Rouyn–Noranda.

## Materials and Methods

### Sampling

A preliminary sampling program carried out in May 1981 confirmed the existence of a concentration gradient for Cu and Zn in the superficial sediments at sites downstream from the central Rouyn–Noranda smelting complex. Accordingly, 13 sampling stations were established along this concentration gradient: Lake Routhier (LR-09, LR-13, LR-15, LR-16, LR-17), Lake Beauchastel (BE-01, BE-03, BE-13, BE-16), and Lake La Bruère (BR-01, BR-04, BR-06, BR-11). The yellow water lily, *Nuphar variegatum*, was selected as a biomonitor plant species. This choice was suggested by this species' ubiquity and apparent metal tolerance (it was present at all sites) and by its morphology (large rhizome; low surface–volume ratio for the submerged parts of the plant, which should minimize metal uptake from the water column). Although the ability of *Nuphar* to absorb and translocate metals has not been demonstrated, Twilley et al. (1977) did report bidirectional movement of P in laboratory experiments with native plants; the acropetal pathway (roots to leaves) dominated.

In late July 1981 five plant specimens were selected at each sampling site, within an area of $<700\ m^2$ (sampling radius $<15$ m), and a short sediment core (10 cm) was collected at the base of each plant. The sediment cores were extruded in the field and the 0- to 2-cm strata were removed, sealed in individual polyethylene bags, cooled to ~0°C in an ice–water mixture, and returned to the central laboratory for immediate processing (see below). The individual plants were harvested, scrubbed gently in lake water, sealed in polyethylene bags, and returned to the laboratory in coolers ($T \sim 4$°C). In the laboratory the leaves, stems, and rhizome of each plant were separated and a section corresponding to the previous year's growth was removed from the rhizome and saved (the remainder of the rhizome was discarded). The leaves were also discarded, as it was feared that metal concentrations in these organs might be influenced by atmospheric deposition of metals directly on the exposed leaf surface. The remaining stem and rhizome samples were dried to constant weight at 105°C and then homogenized in a mechanical blender (Osterizer Cyclotrol 8, model Galaxie). Composite samples of stem tissue were then prepared by combining equal portions from each of the five plants collected at a given site; composite samples of rhizome tissue were prepared in a similar manner. Within-site variation was evaluated at two sites in Lake Routhier (see below).

### Analytical Procedures

*General*

All reagents used in this study were of analytical grade or better. Deionized water for the preparation of stock solutions and the dilution of concentrated digestion solutions was obtained from a Milli-Q3R0/Milli-Q2 system (Millipore Corp.). To minimize metal contamination, labware was soaked in 10% nitric acid for at least 24 h and then rinsed carefully with deionized water before use. Teflon beakers were used for all digestions involving hot concentrated acids.

*Plants*

The composite samples (~1 g) of stem or rhizome tissue were treated with concentrated nitric acid (10 mL) at room temperature for 12 h, warmed to 50°C, and then allowed to cool back to room temperature. Perchloric acid (3 mL) was added and the solutions were heated on a hot plate until perchloric acid fumes appeared. The cooled digestion mixtures were diluted to 10 mL with dilute nitric acid (final concentration 2% $HNO_3$) and analysed for Cu and Zn by flame atomic absorption spectrophotometry (Varian Techtron, model 575 ABQ). The accuracy of this procedure was verified regularly by subjecting a standard sample to the overall analytical procedure (U.S. National Bureau of Standards, sample No. 1570, standard spinach leaves). The analytical precision, as determined by replicate analysis of several samples of *N. variegatum* plant tissue, was generally in the range ±5–10%.

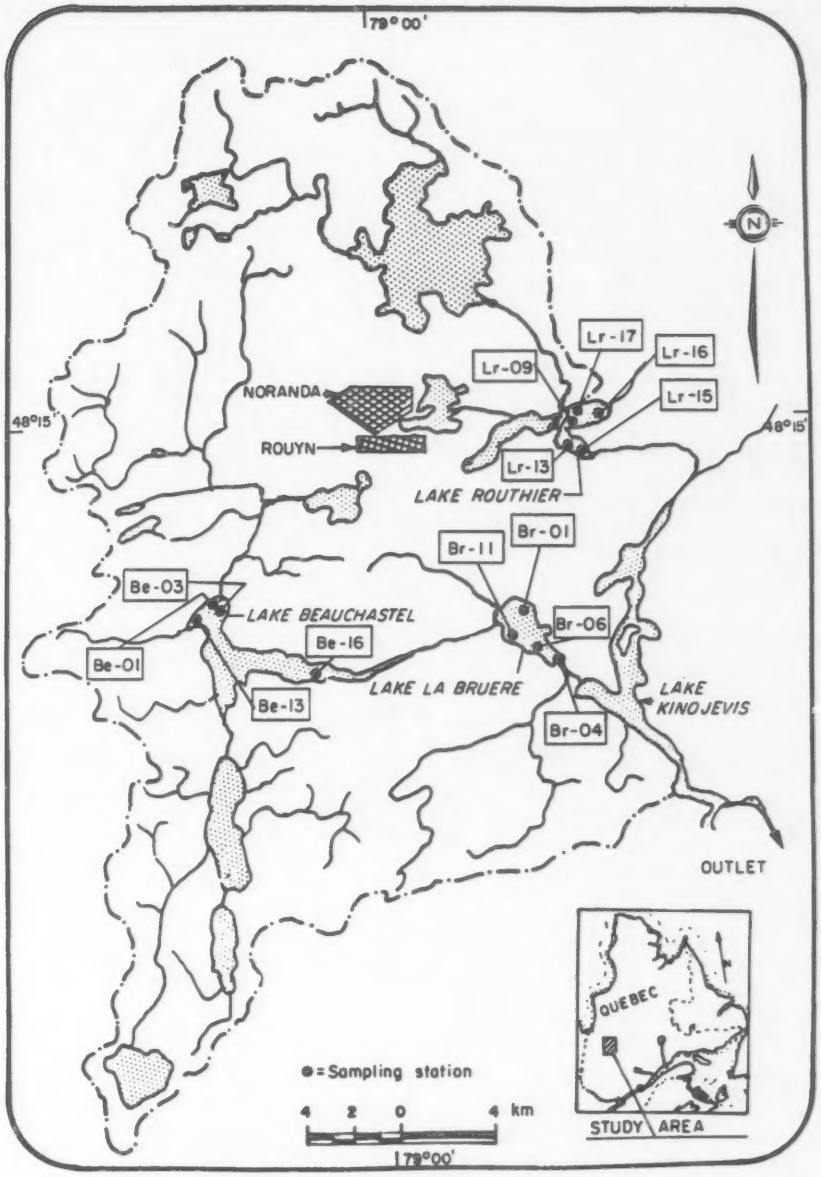



FIG. 1. Location of the study area.

*Sediments*

Sediment samples were wet sieved to remove coarse material (850-μm nylon screen). Composite samples were prepared for each site by pooling equal portions of the 0- to 2-cm stratum from each of the five individual cores. This stratum corresponds to the upper portion of the zone occupied by the plant rhizome, which normally lies horizontally just below the sediment–water interface. These samples were stored at ~4°C in the dark in sealed polyethylene bags until needed for analysis; all efforts were made to minimize the delay between sampling and analysis (maximum delay 7 d).

A portion of each of these composite samples (2.5–3.0 g wet wt.; equivalent to ~1.5 g dry wt.) was subjected to a sequential leaching procedure designed to partition the particulate trace metals into the following five fractions:

(a) M(F1): *exchangeable metals*. The sediment sample was extracted for 10 min with 0.5 mol/L $MgCl_2$ at pH 7.0.

(b) M(F2): *metals bound to carbonates or specifically adsorbed*. The residue from (a) was leached for 5 h with 1 mol/L sodium acetate (NaOAc) adjusted to pH 5.0 with acetic acid (HOAc).

(c) M(F3): *metals bound to Fe–Mn oxides*. The residue from (b) was extracted for 6 h at 95°C with 0.04 mol/L $NH_2OH \cdot HCl$ in 25% (v/v) HOAc.

(d) M(F4): *metals bound to organic matter and sulfides*. The residue from (c) was extracted at 85°C for 5 h with 30% $H_2O_2$

adjusted to pH 2 with $HNO_3$ and then at room temperature with 3.2 mol/L $NH_4OAc$ in 20% (v/v) $HNO_3$.

(e) M(F5): *residual metals*. The residue from (d) was digested with a 5:1 mixture of hydrofluoric and perchloric acids.

The details of this experimental procedure and an evaluation of its precision and accuracy have been published elsewhere (Tessier et al. 1979, 1980). Trace metal concentrations in the leachates were determined by flame atomic absorption spectrophotometry (Varian Techtron, model 575 ABQ), and quantification was achieved with appropriate calibration curves prepared with the components of each extraction solution.

A second portion of each composite sediment sample was removed, dried at 105°C to constant weight, and analysed for a number of complementary parameters. Si and Al concentrations were determined by atomic absorption spectrophotometry (nitrous oxide – acetylene flame), after fusion with lithium metaborate followed by dissolution of the fused material in 1.2 mol/L HCl. Particulate S and C were determined with a Leco Total Sulfur Analyzer (model IR-32) and a Leco Total Carbon Analyzer (model IR-12), respectively. Inorganic C was assumed to be equal to the difference between total and organic C concentrations, the latter being measured after acid treatment (6 mol/L HCl; 30 min) of the sediment to dissolve the carbonates present.

### Analytical Variability

During the preliminary phase of the project, in May 1981, to evaluate the variability of total metal concentrations in the surface sediments at a given sampling site, we collected five separate sediment samples with an Ekman dredge at each of three representative sites. A subsample was removed from the undisturbed surface near the centre of each grab sample, digested with hot concentrated nitric acid, and analysed for "total" Cu and Zn. Within the area sampled at a given site (~50 $m^2$), the relative standard deviation for total metal concentrations in the sediments varied from 5 to 20%. The analytical precision, determined from replicate determinations of total metal concentrations in subsamples from several dried sediment samples, was about ±5%.

To determine the variability of Cu and Zn concentrations within different parts of a particular plant specimen, we selected individual plants from each lake for preliminary analyses. After separation of the stems and rhizome, the latter was further dissected into 1-yr growth sections corresponding to the plant material formed most recently (0 = attached to stems) and to the tissues formed during the preceding two growth periods (designated +1 and +2). The demarcation between growth sections was based on a count of the number of scars visible on the rhizome surface. For example, the portion corresponding to the previous year's growth was estimated by counting back a number of scars equal to the number of petioles attached to the rhizome and produced in the most recent growth period. The analytical results showed appreciable within-plant variability, particularly for Zn (Table 1). Because of the apparent concentration gradient within the rhizome itself, all subsequent rhizome analyses were performed on a standard subsample corresponding to the tissue joined to the stems during the previous growing season (section +1: 1980).

As outlined previously, composite samples of stem and rhizome tissue were normally prepared for each site and then analysed. However, for two sites in Lake Routhier the five specimens were analysed separately, affording an estimate of the variability of Cu and Zn concentrations among plants growing at a particular sampling station. An appreciable inter-plant variability was noted at both stations (Table 2); the relative standard deviations observed for Cu (20–40%) and Zn (5–50%) were considerably greater than the variability attributable to the analytical procedure itself (±5–10%, as determined by replicate analyses).

TABLE 1. Variation of Cu and Zn concentrations (μg/g) within individual specimens of *N. variegatum*.

| | Site BR-06 | | Site BE-13 | | Site LR-13 | |
|---|---|---|---|---|---|---|
| Plant part[a] | Cu | Zn | Cu | Zn | Cu | Zn |
| Stem | 10 | 25 | 4 | 24 | 10 | 94 |
| Rhizome | | | | | | |
| 0 | 10 | 11 | 4 | 15 | 11 | 48 |
| +1 | 9 | 6 | 3 | 13 | 6 | 19 |
| +2 | 11 | 6 | 3 | 9 | 3 | 16 |

[a]See text for details.

## Results and Discussion

### Sediment Analyses

Total concentrations of sediment-bound Cu and Zn, M(S5), generally declined in the sequence Lake Routhier > Lake La Bruère > Lake Beauchastel (Table 3); considerable spatial variation was evident within each lake, however, and the concentration ranges for each lake overlapped. The highest concentrations were observed at stations LR-09 and LR-13, and the lowest at stations BE-03, BR-06, and LR-16. Over the whole study area, the ratio of maximum to minimum concentration for total Cu (~55) was slightly greater than for Zn (ratio ~25). A somewhat greater variation was observed when the individual nondetrital fractions were considered (F1–F4); the corresponding ratios ranged from >400 (M(F1)) to 20–25 (M(F3)). Concentrations of organic and inorganic C, S, and total Fe exhibited less variability, whereas those of Al and Si were practically constant.

With reference to the metal partitioning results shown in Table 3, it should be noted that the distribution of a given metal among various fractions, as obtained with the present sequential extraction scheme, does not necessarily reflect the scavenging action of discrete sediment phases, but rather should be considered as operationally defined by the methods of extraction (Rendell et al. 1980; Tessier et al. 1979). The five fractions have accordingly been assigned numerical designations (M(F1), M(F2), ... M(F5)) rather than precise geochemical descriptions.

TABLE 2. Variability of Cu and Zn concentrations in specimens of *N. variegatum* collected at a given sampling site (Concentrations are expressed as mean ± standard deviation ($N$ = 5); relative standard deviations are given in parentheses (%).).

| Site | Plant part | [Cu] (μg/g) | [Zn] (μg/g) |
|---|---|---|---|
| LR-09 | Stem | 16.1±3.5 (22) | 93.0±13.2 (14) |
| | Rhizome | 7.1±2.4 (34) | 13.5±7.2 (53) |
| LR-15 | Stem | 11.9±4.7 (40) | 76.1±3.5 (5) |
| | Rhizome | 6.0±1.6 (27) | 22.4±6.6 (29) |

As observed in previous studies (Förstner and Wittmann 1981; Tessier et al. 1980, 1982), both Cu and Zn exhibited a distinctive partitioning pattern among the nondetrital fractions F1–F4. For example, the Cu partitioning results showed the expected predominance of fraction 4 (52 ± 15%), approximately equal contributions from fractions 2 (25 ± 6%) and 3 (24 ± 18%), and very low levels in fraction 1: i.e. F4 > F2 ~ F3 > F1. For Zn a very different pattern emerged: fraction 4 (6 ± 2%) was the least important form, fraction 3 dominated the distribution (56 ± 12%), and lower but appreciable proportions were present in fractions 1 (23 ± 14%) and 2 (16 ± 4%), i.e. F3 > F1 ~ F2 > F4.

## Cu and Zn Levels in *Nuphar variegatum*

The Cu and Zn concentrations found in *N. variegatum* in our study area (Table 4) were comparable with those reported for this species in other regions contaminated by mining and smelting activities (Table 5). Compared with the total metal concentrations in the lake sediments, the levels found in the plant tissue were low; mean concentration factors calculated on this basis, i.e. $[M_p]/[M_{sed}]$, were invariably less than 1.0 (e.g. 0.08 ± 0.09 for Cu, 0.18 ± 0.27 for Zn).

Metal concentrations varied appreciably among plants collected at a particular sampling site (Table 2). A literature search failed to yield any comparable estimates of within-site variability for *N. variegatum*, but the observation of such intra-station fluctuations in metal levels (coefficients of variation of ~30% for Cu, ~25% for Zn) is not without precedent for other aquatic plants (Gommes and Muntau 1981a; Welsh and Denny 1980; Harding and Whitton 1981). Possible explanations for this variability include the existence of distinct microhabitats within the sampling site (Harding and Whitton 1981), the collection of specimens of differing age, and the sampling of plants at slightly different stages in their growth cycle; variations in trace metal levels in plants, as a function of the annual growth cycle, are well documented (Mayes and McIntosh 1975; Mayes et al. 1977; Mudroch and Capobianco 1978; Ray and White 1979; Larsen and Schierup 1981).

The distribution of metals within a given plant was far from homogeneous, particularly in the case of Zn. Metal concentrations in the stem generally exceeded those in the rhizome, but the ratios of $[M_{stem}]:[M_{rhizome}]$ varied considerably (Table 4: column S/R). Similar results were reported for *N. variegatum* collected at eight sites in Wanapitei Bay, Ont., where S/R ratios varied from 0.4 to 3.6 for Cu and from 1.0 to 4.0 for Zn (Hutchinson et al. 1975). In the data from the present study, as in those from Wanapitei Bay, the S/R ratios for Zn tended to be higher at stations where the sediments were more highly contaminated (Fig. 2A; $r = 0.73$, $P < 0.002$); a similar but less pronounced trend was evident for Cu (Fig. 2B; $r = 0.54$, $P < 0.036$), provided that the anomalous stem–rhizome pair from the station BR-11 was excluded. The high Cu content of the stems collected at this site (50.4 ± 2.8 μg/g; $N = 5$), together with the normal Cu levels in the rhizomes, led to an abnormally high S/R ratio.

Differences in Zn concentration existed not only between stems and rhizome, but also within the rhizome (Table 1). No reference to this longitudinal variation within the rhizome could be found in the literature for *N. variegatum*, nor for other macrophytes forming rhizomes. However, several workers have reported the existence of such concentration differences in the aerial parts of emergent macrophytes. For example, Larsen and

TABLE 3. Physicochemical characteristics of the sediment samples collected at the different sampling sites: partitioning of Cu, Zn, and Fe as determined with the sequential extraction procedure; organic C, inorganic C, S, Al, and Si concentrations (All the results are based on sediment dry weight; [M(F1)] ... [M(F5)] represent metal concentrations in fractions 1 ... 5 following the sequence given in the text; [M(S5)] represents the sum of metal concentrations for the five fractions, i.e. total metal concentration).

| Site | [M(F1)] (μg/g) | | | [M(F2)] (μg/g) | | | [M(F3)] (μg/g) | | | [M(F4)] (μg/g) | | | [M(F5)] (μg/g) | | | [M(S5)] (μg/g) | | | Org. C (%) | Inorg. C (%) | S (%) | Al (%) | Si (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cu | Zn | Fe | Cu | Zn | Fe | Cu | Zn | Fe | Cu | Zn | Fe | Cu | Zn | Fe | Cu | Zn | Fe | | | | | |
| BE-01 | 1.8 | 37.9 | 1.7 | 12.5 | 14.3 | 294 | 11.4 | 44.2 | 3 470 | 23.1 | 3.1 | 150 | 14.0 | 26.7 | 15 700 | 62.8 | 126 | 19 600 | 0.55 | 0.63 | 0.06 | 11.8 | 71.0 |
| BE-03 | 0.4 | 9.6 | <0.8 | 5.6 | 7.6 | 107 | 7.1 | 22.2 | 1 710 | 3.9 | 0.8 | 43.3 | 6.0 | 23.4 | 15 000 | 23.0 | 63.6 | 16 900 | 0.11 | 0.14 | 0.03 | 11.6 | 74.3 |
| BE-13 | 0.3 | 43.9 | <0.9 | 21.4 | 53.9 | 424 | 13.7 | 131 | 5 620 | 45.0 | 10.7 | 335 | 30.7 | 55.0 | 18 300 | 111 | 295 | 24 700 | 1.06 | 1.22 | 0.08 | 12.9 | 64.7 |
| BE-16 | <0.1 | 14.3 | <0.9 | 5.9 | 17.6 | 80.4 | 7.8 | 59.2 | 3 730 | 15.5 | 5.2 | 236 | 16.7 | 54.0 | 25 300 | 45.9 | 150 | 29 300 | 0.97 | 0.68 | 0.06 | 12.2 | 61.5 |
| BR-01 | 0.1 | 10.6 | <0.9 | 13.9 | 20.3 | 152 | 18.8 | 80.6 | 4 160 | 21.9 | 7.1 | 154 | 25.0 | 51.7 | 20 700 | 79.7 | 170 | 25 200 | 0.61 | 0.56 | 0.04 | 12.9 | 67.5 |
| BR-04 | 1.1 | 55.7 | 1.8 | 25.0 | 38.9 | 282 | 9.0 | 101 | 4 170 | 139 | 16.7 | 907 | 40.7 | 57.7 | 19 000 | 215 | 270 | 24 400 | 2.61 | 1.44 | 0.12 | 12.0 | 61.8 |
| BR-06 | <0.1 | 2.6 | <0.8 | 5.5 | 8.0 | 66.8 | 7.4 | 25.6 | 1 800 | 5.8 | 1.2 | 53.8 | 6.7 | 26.0 | 13 300 | 25.4 | 63.4 | 15 200 | 0.16 | 0.16 | 0.03 | 11.3 | 73.6 |
| BR-11 | 0.4 | 16.8 | 0.9 | 33.8 | 39.2 | 180 | 45.9 | 168 | 7 930 | 65.0 | 23.1 | 376 | 61.3 | 106 | 25 700 | 206 | 353 | 34 200 | 1.12 | 1.43 | 0.07 | 13.6 | 58.7 |
| LR-09 | 53.6 | 461 | 28.3 | 179 | 138 | 1520 | 12.4 | 368 | 18 100 | 424 | 40.3 | 815 | 82.0 | 110 | 29 000 | 751 | 1117 | 49 500 | 1.13 | 1.85 | 0.16 | 13.4 | 57.1 |
| LR-13 | 18.4 | 274 | 7.2 | 101 | 108 | 650 | 12.6 | 343 | 6 740 | 217 | 45.6 | 627 | 63.0 | 99.0 | 27 700 | 412 | 870 | 35 700 | 1.16 | 1.35 | 0.09 | 14.0 | 58.3 |
| LR-15 | 3.3 | 116 | 1.8 | 50.2 | 84.7 | 415 | 16.6 | 326 | 5 590 | 120 | 48.3 | 439 | 56.7 | 113 | 26 000 | 247 | 688 | 32 400 | 1.09 | 0.99 | 0.06 | 13.8 | 60.0 |
| LR-16 | <0.1 | 1.1 | <0.9 | 0.8 | 2.0 | 86.8 | 2.2 | 14.7 | 2 300 | 3.5 | 1.4 | 112 | 6.7 | 26.7 | 14 000 | 13.2 | 45.9 | 16 500 | 0.39 | 0.34 | 0.03 | 11.7 | 72.2 |
| LR-17 | 21.8 | 77.9 | 7.2 | 54.2 | 20.9 | 721 | 15.7 | 77.8 | 7 690 | 105 | 14.1 | 630 | 55.7 | 80.3 | 26 700 | 252 | 271 | 35 700 | 1.31 | 1.43 | 0.08 | 13.6 | 57.7 |
| Mean[a] | 4.2 | 86.3 | 7.3 | 39.1 | 42.6 | 383 | 13.9 | 135 | 5 620 | 91.4 | 16.7 | 375 | 35.8 | 63.8 | 21 300 | 188 | 345 | 27 600 | 0.94 | 0.94 | 0.07 | 12.7 | 64.5 |
| SD | 7.2 | 135 | 13.7 | 50.4 | 42.6 | 403 | 10.6 | 128 | 4 280 | 119 | 17.3 | 290 | 25.7 | 34.2 | 5 700 | 207 | 338 | 9 840 | 0.64 | 0.56 | 0.04 | 1.0 | 6.5 |

[a]For the purposes of calculating mean concentrations, concentrations lower than the analytical detection limit were assigned values = ½ the detection limit.

TABLE 4. Cu and Zn concentrations in the samples of *N. variegatum* collected at the different sampling sites (Composite samples were analysed at all sites except LR-09 and LR-15; samples collected at these sites were analysed separately and mean values are reported here (cf. Table 2)).

| | [Cu] (μg/g) | | | [Zn] (μg/g) | | |
|---|---|---|---|---|---|---|
| Site | Stem | Rhizome | Ratio S/R | Stem | Rhizome | Ratio S/R |
| BE-01 | 9.2 | 5.5 | 1.7 | 26.5 | 16.9 | 1.6 |
| BE-03 | 7.0 | 4.6 | 1.5 | 23.4 | 49.8 | 0.5 |
| BE-13 | 5.1 | 3.7 | 1.4 | 27.2 | 9.9 | 2.7 |
| BE-16 | 4.7 | 3.0 | 1.6 | 20.5 | 9.5 | 2.2 |
| BR-01 | 10.6 | 5.9 | 1.8 | 29.8 | 42.4 | 0.7 |
| BR-04 | 6.1 | 3.9 | 1.6 | 22.5 | 8.1 | 2.8 |
| BR-06 | 8.1 | 5.4 | 1.5 | 22.8 | 11.8 | 1.9 |
| BR-11 | 50.4 | 3.6 | 14.0 | 60.4 | 20.3 | 3.0 |
| LR-09 | 16.1 | 7.1 | 2.3 | 93.0 | 13.5 | 6.9 |
| LR-13 | 10.0 | 7.9 | 1.3 | 77.8 | 12.6 | 6.2 |
| LR-15 | 11.9 | 6.0 | 2.0 | 76.1 | 22.4 | 3.4 |
| LR-16 | 2.4 | 3.5 | 0.7 | 23.6 | 37.2 | 0.6 |
| LR-17 | 37.3 | 12.1 | 3.1 | 63.2 | 15.2 | 4.2 |
| Mean | 13.0 | 5.6 | | 43.6 | 20.7 | |
| SD | 14.4 | 2.5 | | 26.3 | 13.6 | |

Schierup (1981) noted that concentrations of Zn (but not Cd, Cu, or Pb) in the stems of *Phragmites australis* were much higher in the terminal 20–40 cm than in the parts of the plant closer to the sediment–water interface. The opposite trend was reported for *Typha latifolia* by Mudroch amd Capobianco (1978), who noted that Cu and Ni concentrations were lower in the stem tips (0–40 cm) than in the adjacent sections (40–70 cm).

## Sediment–Plant Relationships

To facilitate the discussion of relationships between metal concentrations in *N. variegatum* and those in the adjacent lake sediments, consider the following conceptual model: the sediment-bound metal is partitioned among the five operationally defined fractions, M(F1) ... M(F5), one or more of which may be in equilibrium with $M_i$, the metal present in the interstitial water. Some fraction of $M_i$, depending on the environmental conditions prevailing in the interstitial water (e.g. [ligands], pH), exchanges with $M_a$, metal bound at the rhizome (root) surface. After transport into the plant, the metal enters the dissolved intracellular pool, from which it may be removed and stored within the rhizome itself or translocated towards the stem and eventually stored there. This scheme *neglects* possible metal uptake from the water column into the submerged plant parts; this latter assumption is discussed below.

Two predictions follow from this simplified scheme for metal accumulation. (1) We would expect to find a proportionality between $M_a$ and those metal fractions (M(F1), M(F2), ...) in adsorptive equilibrium with $M_i$. If metal uptake into the rhizome (root) depends on the metal concentration at the rhizome (root) surface (Barber and Claassen 1977; Gommes and Muntau 1981b) the higher concentration of $M_a$ would be expected to be associated with a higher metal flux into the rhizome and hence higher values for metal stored in the rhizome. A relationship should then exist between the measured metal concentration in the rhizome, $[M_r]$, and one or more of the metal fractions in the sediments. (2) If metal uptake via the root–rhizome system is

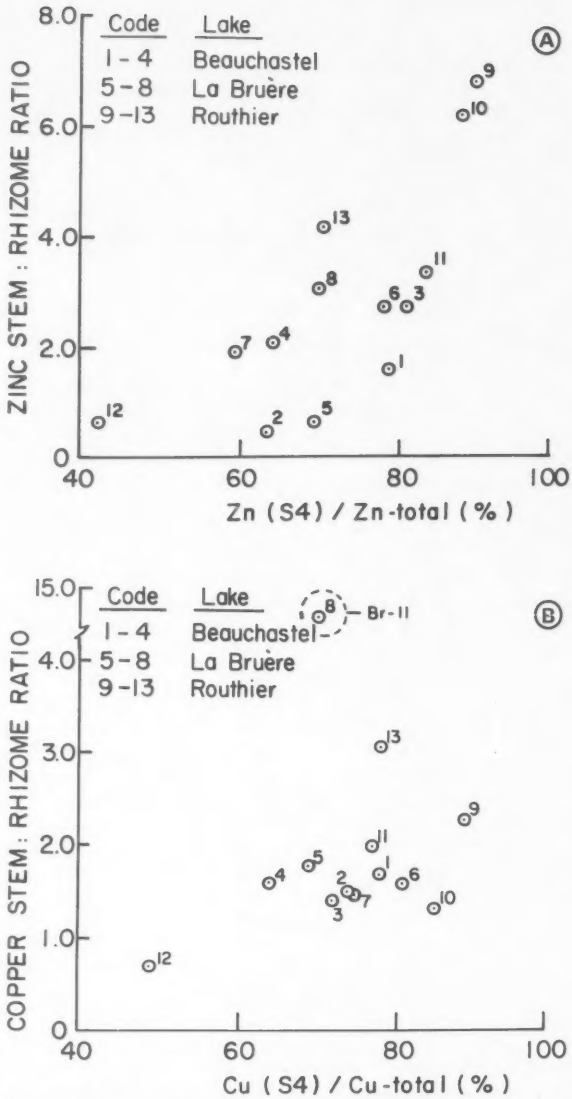



FIG. 2. Variation of stem:rhizome metal concentration ratios in *N. variegatum* as a function of anthropogenic contamination of the adjacent sediments. Percent nonresidual metal is used as an index of anthropogenic influence. (a) Zn; (b) Cu.

followed by translocation of the metal to binding sites in both the rhizome and the stem, then metal concentrations in the rhizome and stem should be positively correlated.

To test the first of these predictions we compared measured Cu and Zn concentrations in the rhizome ($[Cu_r]$, $[Zn_r]$) with factors related to metal concentrations in the sediment, the rationale being that if metal uptake occurs via the root–rhizome system, then $[M_r]$ should serve as a good "integrator" of metal availability in the sediments (Chiaudani 1969; Welsh and Denny 1980; Schierup and Larsen 1981). The sediment factors included the metal concentration in each of the five fractions obtained with the sequential extraction procedure ([M(F1)] ... [M(F5)]), the sum of these fractions ([M(S5)] = total metal

TABLE 5. Cu and Zn concentrations in *N. variegatum*: comparison with literature values.

| Plant part | [Cu] (μg/g) | [Zn] (μg/g) | Sampling area | Reference |
|---|---|---|---|---|
| Stem | 2–50 | 21–93 | Lakes; | Present study |
| Rhizome | 3–12 | 8–50 | Rouyn–Noranda (Quebec) | |
| Stem | 2–23 | 16–35 | Wanapitei Bay | Hutchinson et al. 1975 |
| Roots | 2–12 | 6–29 | (Ontario) | |
| Stem and leaves | 4–7 | 11–274 | Lakes; Flin-Flon (Manitoba) | Franzin and McFarlane 1980 |
| Whole plant | 15–22 | 35–65 | Several rivers (Pennsylvania) | Adams et al. 1973 |

TABLE 6. Correlation coefficients between the metal content of *N. variegatum* and the metal concentrations in the adjacent lake sediments. Values significantly different from zero at the 1% (italicized) and 5% (regular type) levels are distinguished from those not significantly different from zero at the 5% level (in parentheses). Thirteen sites were considered in all cases except those involving Cu(F1), for which $N = 10$.

| Metal | Plant part | Sediment fraction | | | | | |
|---|---|---|---|---|---|---|---|
| | | M(F1) | M(F2) | M(F3) | M(F4) | M(F5) | M(S5) |
| Cu | Rhizome | 0.55 | 0.49 | (0.01) | (0.40) | 0.48 | (0.45) |
| | Stem | (0.12) | (0.22) | *0.85* | (0.15) | 0.55 | (0.26) |
| Zn | Rhizome | (−0.31) | (−0.37) | (−0.31) | (−0.31) | (−0.35) | (−0.34) |
| | Stem | *0.81* | *0.84* | *0.89* | *0.90* | *0.90* | *0.91* |

TABLE 7. Correlation coefficients between the metal content of *N. variegatum* rhizomes and the metal concentrations in sediment fractions M(F1) and M(F2): effect of normalization with respect to Fe. Values significantly different from zero at the 1% (italicized) and 5% (regular type) levels are distinguished from those not significantly different from zero at the 5% level (in parentheses).

| Metal | Sediment fraction | | | | | |
|---|---|---|---|---|---|---|
| | M(F1) | M(F1)/Fe(F1) | M(F1)/Fe(F3) | M(F2) | M(F2)/Fe(F2) | M(F2)/Fe(F3) |
| Cu | 0.55 | *0.94* | *0.82* | 0.49 | (0.17) | 0.58 |
| Zn | (−0.31) | (0.33) | (−0.35) | (−0.37) | (−0.31) | (−0.35) |

concentration in the sediments), and finally these concentrations normalized with respect to either the reducible Fe content of the sediments ([M(F*n*)] ÷ [Fe(F3)]) or the concentration of extractable Fe ([M(F*n*)] ÷ [Fe(F*n*)]). Correlation coefficients were calculated in each case and the data were examined graphically to verify dispersion and linearity. To test the second prediction we looked for relationships between metal concentrations measured in the rhizome, [$M_r$], and those measured in the stem, [$M_s$].

*Copper*

No statistically significant correlations were observed between the Cu content of the rhizomes and the total Cu concentration in the substrate. A similar lack of correlation was noted in the only previous study of metal levels in *N. variegatum* in which metal concentrations were determined in both the plant tissues and the adjacent lake sediment (Hutchinson et al. 1975). However, if the partitioning of Cu in the lake sediment was considered, several statistically significant correlations did appear (Table 6), notably between [$Cu_r$] and the concentrations of Cu in the fractions most readily extracted from the sediments, [Cu(F1)] and [Cu(F2)]. As indicated in Table 7, the correlation between [$Cu_r$] and [Cu(F1)] improved when the latter was divided by the concentration of exchangeable Fe, [Fe(F1)]. However, this relationship is based on only seven sampling sites (Fig. 3), since the concentrations of exchangeable Cu and/or exchangeable Fe were less than the analytical detection limit at six of the stations. Such an inverse relationship with [Fe(F1)] might be anticipated if Fe and Cu compete for uptake sites, e.g. at the rhizome (root) surface. Correlation coefficients also increased when the concentrations of Cu in fractions 1 or 2 were normalized with respect to the iron oxyhydroxide content of the sediment, [Fe(F3)]. The existence of a relationship between [$Cu_r$] and the ratio [Cu(F1)]/[Fe(F3)] or [Cu(F2)]/[Fe(F3)] implies that, for a given value of [Cu(F1)] or [Cu(F2)] in the sediment, the Cu content of the rhizome is inversely proportional to the concentration of amorphous iron oxide. An analogous protective role has been suggested for iron oxyhydroxides in the regulation of Cu, Pb, and Zn bioavailability to estuarine and freshwater molluscs (Luoma and Bryan 1978; Tessier et al. 1984).

The next relationship to be examined was that between the Cu

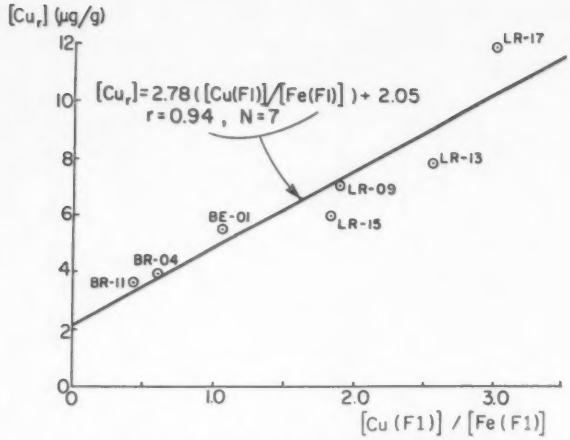



FIG. 3. Relationship between the Cu content of the rhizomes of *N. variegatum* and the ratio of exchangeable Cu to exchangeable Fe in the adjacent sediments.

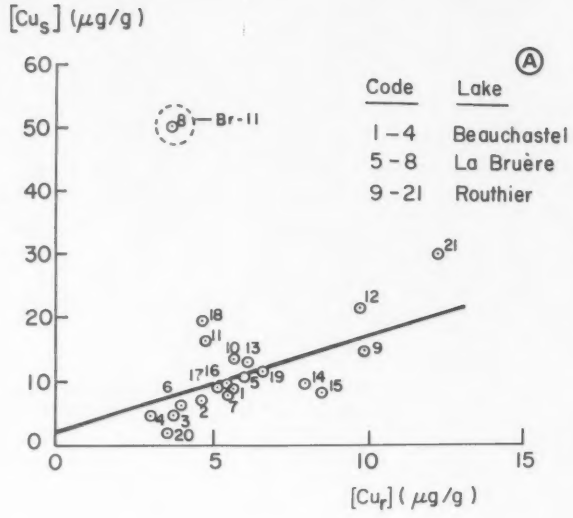
content of the stems and the Cu concentration in the rhizome. The relationship between [$Cu_s$] and [$Cu_r$] was statistically significant, provided that the stem–rhizome pair from station BR-11 was again excluded (Fig. 4A; $r = 0.72$, $P < 0.005$, $N = 21$). This correlation is consistent with the hypothesis of a translocation pathway from rhizome to stem.

*Zinc*

In contrast with the results for Cu, no relationship could be discerned between the Zn content of the rhizomes and any of the Zn fractions in the sediment, even after normalization of the latter values with respect to Fe (Tables 6 and 7). Equally noteworthy is the lack of any correlation between the Zn concentration in the rhizomes and that of the stems (Fig. 4B). Obviously there is no evidence in the present data that Zn accumulates in *N. variegatum* via the sediments; the original scheme for metal accumulation in this plant is clearly inadequate.

Numerous correlations *were* observed between the Zn content of the stems and each of the Zn fractions in the sediment (Table 6). Based on this statistical analysis, however, it is difficult to associate bioavailability of sediment-bound Zn to particular phases of the sediment; intercorrelations between the various Zn fractions in the sediments are frequently observed. The difficulty in identifying key geochemical phases is compounded by the fact that the metal partitioning obtained with the extraction scheme is operationally defined by the reagents and conditions used for the extractions.

Visual inspection of the plots of [$Zn_s$] against [Zn(F*n*)] suggested the existence of two groups of plants (e.g. Fig. 5A, 5B). In the first group, consisting of plants with relatively low Zn content that had been collected at the less contaminated sites, there was no apparent relationship between [$Zn_s$] and [Zn(F*n*)]. For the second group, however, Zn levels were considerably higher in both the sediments and the stems, and a direct relationship between [$Zn_s$] and [Zn(F*n*)] was evident. As mentioned above, no relationships were found at these sites between [$Zn_r$] and [Zn(F*n*)], nor between [$Zn_r$] and [$Zn_s$]. Hence, we are led to speculate that (i) the water lily accumulates Zn directly from the water column and (ii) there exists an exchange mechanism between the interstitial water in the sediments and the overlying water column. Just such a



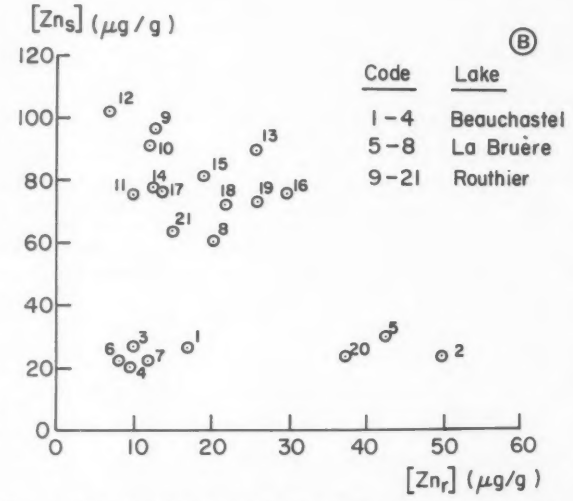




FIG. 4. Relationship between the metal content of the stems of *N. variegatum* and the metal concentration in the corresponding rhizomes. (a) Cu; (b) Zn.

mechanism was proposed by Welsh and Denny (1980) to explain an apparent contradiction between laboratory and field results for Pb accumulation in two *Potamogeton* species. In a field study these workers found that Pb concentrations in plant shoots were correlated with metal levels in the sediments, yet in the laboratory they were able to show that translocation of Pb from the roots to the shoot does not occur. Loss of Pb from the sediments to the immediately overlying water was postulated to occur, either by continuous diffusion or by periodic release caused by turbulent mixing at the sediment–water interface. The present results suggest that this type of exchange may also be involved in the accumulation of Zn by *N. variegatum*.

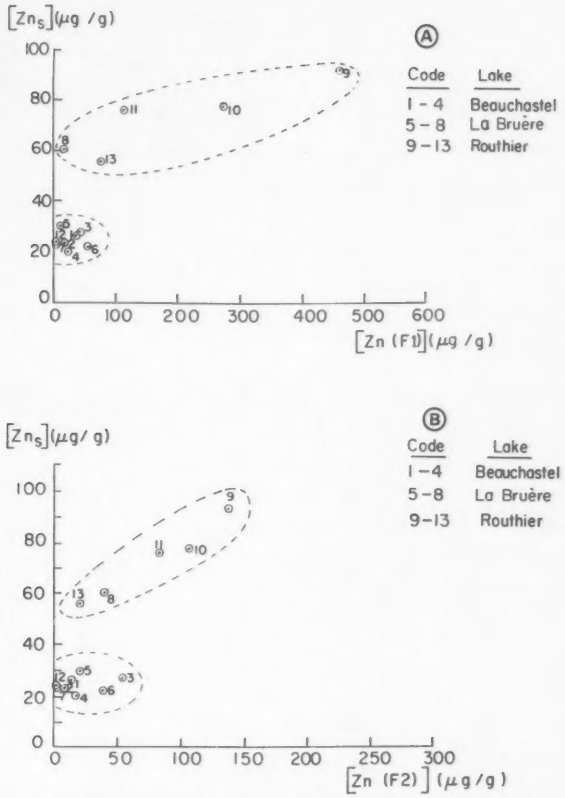



FIG. 5. Relationship between the Zn content of the stems of *N. variegatum* and the Zn concentration in the adjacent sediments. (a) [Zn(F1)]; (b) [Zn(F2)].

## General Discussion

The present study illustrates the important role played by sediments in controlling the accumulation of metals in the yellow water lily, *N. variegatum*. For Cu, a significant portion of the metal burden in the plant appears to be derived from the adjacent lake sediments themselves, via a pathway involving metal uptake into the rhizome and subsequent translocation to the stems. The results also suggest, however, that most of the Zn in the plant stems is derived directly from the water column; in this case we postulate that metal concentrations in the loosely bound fractions of the surficial sediment are in equilibrium with the metal concentrations in the water column and thus only indirectly influence metal accumulation in the plant. It should be emphasized that these conclusions strictly apply only to the particular set of field conditions that prevailed in our study area. The confirmation of these suggestions must await verification under controlled conditions.

## Acknowledgements

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## References

ADAMS, F. S., H. COLE, AND L. B. MASSIE. 1973. Element constitution of selected aquatic vascular plants from Pennsylvania: submerged and floating leaved species and rooted emergent species. Environ. Pollut. 5: 117–147.

AUCLAIR, A. N. D. 1979. Factors affecting tissue nutrient concentrations in a *Scirpus–Equisetum* wetland. Ecology 60: 337–348.

AULIO, K. 1980. Accumulation of copper in fluvial sediments and yellow water lilies (*Nuphar lutea*) at varying distances from a metal processing plant. Bull. Environ. Contam. Toxicol. 25: 713–717.

BARBER, S. A., AND N. CLAASSEN. 1977. A mathematical model to simulate metal uptake by plants growing in soil, p. 358–364. *In* H. Drucker and R. E. Wildung [ed.] Biological implications of metals in the environment. U.S. Energy Res. Dev. Admin. Symp. Ser. Vol. 42.

BOYD, C. E. 1978. Chemical composition of wetland plants, p. 155–167. *In* R. E. Good, D. F. Whigham, and R. L. Simpson [ed.] Freshwater wetlands — ecological processes and management potential. Academic Press, New York, NY.

CHIAUDANI, G. 1969. Contenuti normali ed accumuli di rane in *Phragmites communis* L come risposta a quelli nei sedimenti di sei laghi italiani. Mem. Ist. Ital. Idrobiol. 25: 81–95.

DENNY, P. 1980. Solute movement in submerged angiosperms. Biol. Rev. 55: 65–92.

DIETZ, F. 1973. The enrichment of heavy metals in submerged plants, p. 53–62. *In* S. H. Jenkins [ed.] Advances in water pollution research. Pergamon Press, Oxford, U.K.

DYKYJOVA, D. 1979. Selective uptake of mineral ions and their concentration factors in aquatic higher plants. Folia Geobot. Phytotaxon. Praha 14: 267–325.

FÖRSTNER, U., AND G. T. W. WITTMANN. 1981. Metal pollution in the aquatic environment, p. 238–246. 2nd ed. Springer-Verlag, Berlin.

FRANZIN, W. G., AND G. A. MCFARLANE. 1980. An analysis of the aquatic macrophyte, *Myriophyllum exalbescens*, as an indicator of metal contamination of aquatic ecosystems near a base metal smelter. Bull. Environ. Contam. Toxicol. 24: 597–605.

GALLAGHER, J. L., AND P. L. WOLF. 1980. Field bioassays for the role of plants as vectors in contaminant transfer from dredged material, p. 445–463. *In* R. A. Baker [ed.] Contaminants and sediments, Vol. 2. Analysis, chemistry and biology. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

GOMMES, R., AND H. MUNTAU. 1981a. La composition chimique des limnophytes du Lac Majeur. Mem. Ist. Ital. Idrobiol. 38: 237–307.

1981b. "Carry-over" des métaux lourds dans un écosystème aquatique. Mem. Ist. Ital. Idrobiol. 38: 379–408.

HARDING, J. P. C., AND B. A. WHITTON. 1978. Zinc, cadmium and lead in water, sediments and submerged plants of the Derwent reservoir, Northern England. Water Res. 12: 307–316.

1981. Accumulation of zinc, cadmium and lead by field populations of *Lemanea*. Water Res. 15: 301–319.

HUTCHINSON, G. E. 1975. The chemical ecology of freshwater macrophytes, p. 264–407. *In* A treatise on limnology. Vol. III. Limnological botany. John Wiley & Sons, New York, NY.

HUTCHINSON, T. C., A. FEDORENKO, J. FITCHKO, A. KUJA, J. VAN LOON, AND J. LICKWA. 1975. Movement and compartmentation of nickel and copper in an aquatic ecosystem. Trace Subst. Environ. Health 9: 89–105.

JENNE, E. A., AND S. N. LUOMA. 1977. Forms of trace elements in soils, sediments and associated waters: an overview of their determination and biological availability, p. 110–143. *In* H. Drucker and R. E. Wildung [ed.] Biological implications of metals in the environment. U.S. Energy Res. Dev. Admin. Symp. Ser. Vol. 42.

KINKADE, M. L., AND H. E. ERDMAN. 1975. The influence of hardness components ($Ca^{2+}$ and $Mg^{2+}$) in water on the uptake and concentration of cadmium in a simulated freshwater ecosystem. Environ. Res. 10: 308–313.

LALONDE, J. P., AND P. LASALLE. 1983. Atlas géochimique de l'argile et du till de base de l'Abitibi. Quebec Ministry of Energy and Resources, Rep. DPV-830: 80 p.

LANGSTON, W. J. 1982. The distribution of mercury in British estuarine sediments and its availability to deposit-feeding bivalves. J. Mar. Biol. Assoc. U.K. 62: 667–684.

LARSEN, V. J., AND H. H. SCHIERUP. 1981. Macrophyte cycling of zinc,

copper, lead and cadmium in the littoral zone of a polluted and a nonpolluted lake. II. Seasonal changes in heavy metal content of aboveground biomass and decomposing leaves of *Phragmites australis* (Cav.) Trin. Aquat. Bot. 11: 211–230.

LEE, C. R., T. C. STURGIS, AND M. C. MCLANDIN. 1976. A hydroponic study of heavy metal uptake by selected marsh plant species. U.S. Army Engineer Waterways Experiment Station, Dredged Material Research Program, DMRP Technical Report D-76-5, Vicksburg, MS, USA: 63 p.

LUOMA, S. N., AND G. W. BRYAN. 1978. Factors controlling the availability of sediment-bound lead to the estuarine bivalve *Scrobicularia plana*. J. Mar. Biol. Assoc. U.K. 58: 793–802.

1979. Trace metal bioavailability: modelling chemical and biological interactions of sediment-bound zinc, p. 577–611. *In* E. A. Jenne [ed.] Chemical modelling — speciation, sorption, solubility and kinetics in aqueous systems. ACS Symp. Ser. No. 93. American Chemical Society, Washington, DC.

MAYES, R., AND A. MCINTOSH. 1975. The use of aquatic macrophytes as indicators of trace metal contamination in freshwater lakes. Trace Subst. Environ. Health 9: 157–167.

MAYES, R. A., A. W. MCINTOSH, AND V. L. ANDERSON. 1977. Uptake of cadmium and lead by a rooted aquatic macrophyte (*Elodea canadensis*). Ecology 58: 1176–1180.

MCINTOSH, A. W., B. K. SHEPPARD, R. A. MAYES, G. J. ATCHINSON, AND D. W. NELSON. 1978. Some aspects of sediment distribution and macrophyte cycling of heavy metals in a contaminated lake. J. Environ. Qual. 7: 301–305.

MILLER, G. E., I. WILE, AND G. G. HITCHIN. 1983. Patterns of accumulation of selected metals in members of soft-water macrophyte flora of central Ontario lakes. Aquat. Bot. 15: 53–64.

MUDROCH, A., AND J. CAPOBIANCO. 1978. Study of selected metals in marshes on Lake St. Clair, Ontario. Arch. Hydrobiol. 84: 87–108.

1979. Effects of mine effluent on uptake of Co, Ni, Cu, As, Zn, Cd, Cr and Pb by aquatic macrophytes. Hydrobiologia 64: 223–231.

RAY, S., AND W. WHITE. 1976. Selected aquatic plants as indicator species for heavy metal pollution. J. Environ. Sci. Health A11: 717–725.

1979. *Equisetum arvense* — an aquatic vascular plant as a biological monitor for heavy metal pollution. Chemosphere 3: 125–128.

RENDELL, P. S., G. E. BATLEY, AND A. J. CAMERON. 1980. Adsorption as a control of metal concentrations in sediment extractions. Environ. Sci. Technol. 14: 314–318.

SCHIERUP, H. H., AND V. J. LARSEN. 1981. Macrophyte cycling of zinc, copper, lead and cadmium in the littoral zone of a polluted and a non-polluted lake. I. Availability, uptake and translocation of heavy metals in *Phragmites australis* (Cav.) Trin. Aquat. Bot. 11: 197–210.

TESSIER, A., P. G. C. CAMPBELL, J. C. AUCLAIR, AND M. BISSON. 1984. Relationships between the partitioning of trace metals in sediments and their accumulation in the tissues of the freshwater mollusc *Elliptio complanata* in a mining area. Can. J. Fish. Aquat. Sci. 41: 1463–1472.

TESSIER, A., P. G. C. CAMPBELL, AND M. BISSON. 1979. Sequential extraction procedure for the speciation of particulate trace metals. Anal. Chem. 51: 844–851.

1980. Trace metal speciation in the Yamaska and St. François rivers (Québec). Can. J. Earth Sci. 17: 90–105.

1982. Particulate trace metal speciation in stream sediments and relationships with grain size: implications for geochemical exploration. J. Geochem. Explor. 16: 77–104.

TWILLEY, R. R., M. M. BRINSON, AND G. J. DAVIS. 1977. Phosphorus absorption, translocation, and secretion in *Nuphar luteum*. Limnol. Oceanogr. 22: 1022–1032.

WELSH, P., AND P. DENNY. 1976. Waterplants and the recycling of heavy metals in an English lake. Trace Subst. Environ. Health 10: 217–223.

1979. The translocation of lead and copper in two submerged aquatic angiosperm species. J. Exp. Bot. 30: 339–345.

1980. The uptake of lead and copper by submerged aquatic macrophytes in two English lakes. J. Ecology 68: 443–455.

# Conversion of Blade Length Increments into Biomass Production Estimates in *Laminaria longicruris*

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Gendron, L. 1985. Conversion of blade length increments into biomass production estimates in *Laminaria longicruris*. Can. J. Fish. Aquat. Sci. 42: 33–37.

Three different methods to convert kelp blade length increments into biomass production estimates were compared for *Laminaria longicruris*. The first two models, the exponential and the chordal models, rely on a generalized blade length to weight relationship, whereas the third, the biomass model, is independent of such generalizations. Differences between the three models were examined for the entire range of blade sizes, for which linear growth was measured during three consecutive 3-wk periods, from June to August 1982. There were no significant differences between the two first models although estimates using the chordal model were constantly and slightly lower (<10%) than those using the exponential model. There were significant differences between the biomass model and the others; the differences increased directly with blade size. Biomass production estimates of larger blades obtained using the biomass model were up to 45% lower than with the exponential model. A correction equation related to blade size, based on estimates obtained using the biomass model, was calculated for the exponential model. The correction equation provides a means for comparing or converting year-round estimates obtained by either methods, for different size-structured populations of *L. longicruris* of sheltered habitats.

Trois différents modèles de conversion de la croissance en longueur des frondes en estimations de production ont été comparés pour *Laminaria longicruris*. Les deux premiers modèles, le modèle exponentiel et le modèle chordal, sont tous deux définis à partir d'une relation générale entre la longueur et le poids des frondes, alors que le troisième, le modèle pondéral, est indépendant de telles généralisations. Les différences entre ces trois modèles ont été examinées sur l'étendue de taille des frondes, pour lesquelles la croissance linéaire a été mesurée pendant trois périodes consécutives de 3 sem, entre juin et août 1982. Aucune différence significative n'apparaît entre les deux premiers modèles. Toutefois, les estimations de production obtenues par le modèle chordal sont de façon constante, légèrement plus basses (<10 %) que celles obtenues par le modèle exponentiel. Des différences significatives apparaissent entre le modèle pondéral et les deux modèles précédents. Ces différences sont liées à la longueur des frondes et s'accentuent avec une augmentation de la taille de celles-ci. Les valeurs de production obtenues par le modèle pondéral pour les plus longues frondes, sont jusqu'à 45 % moins élevées que celles obtenues par le modèle exponentiel. Un facteur de correction basé sur les estimations obtenues par le modèle pondéral et lié à la taille des frondes a été calculé pour le modèle exponentiel. Ce facteur de correction permet de comparer ou de convertir les valeurs de production annuelle obtenues par l'une ou l'autre méthode pour des populations de *L. longicruris* de milieux abrités.

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Procedures for estimating biomass production of kelp species using blade length increments have recently been reviewed by Mann and Mann (1981). Three models converting linear increments into biomass production, each of which had been used on a different species, were then analyzed: an exponential model (I), a chordal model (II), and a biomass model (III).

In the exponential model, the conversion of length increments into biomass production is based on a generalized relationship of the form $W = aL^b$ where length ($L$) and weight ($W$) are derived from observations on a large number of plants. The biomass production ($P_I$) is determined as follows:

$$P_I = a(L_1 + g)^b - aL_1{}^b$$

where $g$ is the linear growth obtained by Parke's (1948) method and $L_1$ is the initial blade length. Because this model does not consider blade erosion, the value of $b$ is inflated and leads to an overestimation of biomass production (Mann and Mann 1981).

Mann (1972) used the exponential model in estimating the biomass production of *Laminaria longicruris* Pyl. in St. Margaret's Bay, Nova Scotia. Various attempts have since been made to find a more reliable estimate of biomass production (Hatcher et al. 1977; Gérard and Mann 1979). Mann et al. (1979) proposed a modification to the first model and based the conversion of length increments into biomass production on a linear, rather than exponential, relationship between blade length and weight, approximately equal to the one occurring at the time of initial measurements. Thus, biomass production ($P_{II}$) was calculated as follows:

$$P_{II} = g[a(L_1 + 1)^b - aL_1{}^b].$$

The chordal model (Mann and Mann 1981) was devised for

type A and B plants of *Ecklonia maxima* where morphology and growth are similar to that of *Laminaria* species (Mann et al. 1979).

In a study on the productivity of *Ecklonia radiata*, Mann and Kirkman (1981) developed the biomass model, which does not rely on extrapolation from a generalized relationship between blade length and weight. They suggested that biomass production could be calculated by multiplying length increment ($g$) by the average weight per unit length ($W/L$) as measured in the blade region of maximum biomass. Values of $W/L$ were obtained by cutting plants transversely into segments and examining the distribution of biomass along the blade. The pattern of biomass distribution revealed three distinct blade regions: first, a zone of growth characterized by increasing $W/L$ values; second, a zone of maximum biomass, where there is no further growth and also no erosion; and third, a zone of erosion where $W/L$ ratio decreases. According to Mann and Mann (1981), applicability of this method could be extended to all laminariales, and specifically to *L. longicruris* for which the distribution of biomass along the blade is similar to that of *E. radiata*.

Although the accuracy of the three models has not been assessed, from the analysis of the exponential model made by Mann and Mann (1981), it appears that models relying on a length to weight relationship overestimate biomass production. Because the biomass model does not rely on such a relationship, it does not reproduce the bias inherent in the first two models and thus overcomes overestimation caused by blade erosion. On this basis, the biomass model can be viewed as a more reliable method for estimating biomass production.

My study was undertaken to provide detailed measurements of the differences between the three models in estimating the productivity of *L. longicruris*, and to estimate the error involved in the use of the exponential and the chordal models, relative to the biomass model, under the assumption that the latter is more accurate.

## Materials and Methods

Field work was carried out at Ruisseau–Leblanc in Baie des Chaleurs, Québec (40°05.2′N; 65°38.4′W). The stand studied was at 4-m depth in a sheltered area, where the mean biomass of *L. longicruris* is $2\,kg \cdot m^{-2}$ (Gendron 1983).

Growth was monitored for three consecutive 3-wk periods from June to August 1982 (Table 1). At the beginning of each period, a number of plants (Table 1) were individually tagged, measured, and a hole was punched in each blade 20 cm above the stipe to permit an assessment of linear growth (see Parke 1948). Plants were selected so that the entire range of blade sizes was represented. At the end of each 3-wk period, remaining plants (Table 1) were collected and immediately brought to a field station where they were measured and weighed (fresh weight). Estimation of biomass production, according to the biomass model, required the determination of the average weight per unit length in the blade region of maximum biomass. Therefore, each plant was cut transversely into segments 2.5–20 cm wide, depending on blade length. The segments were weighed (fresh weight) so that biomass distribution along the blade could be determined.

Biomass production estimates for the exponential and chordal models were calculated using the generalized relationship between blade length ($L$) and blade weight ($W$) derived from the observations made on all plants. The fitted power curve obtained was as follows:

$$W = 0.038L^{1.735}$$

with $r^2 = 0.96$.

TABLE 1. Number of plants of *L. longicruris* tagged at the beginning of each growth period and number remaining at the end of each period.

| Growth periods | Number of plants initially tagged | Number of remaining plants |
|---|---|---|
| 22 June – 13 July | 100 | 91 |
| 14 July – 3 Aug. | 100 | 93 |
| 3–24 Aug. | 50 | 45 |

Estimates were expressed as a function of initial blade weight, and linear regressions were fitted. The initial blade weight was estimated from initial blade length measurements using the power relation defined. For each period, the regression lines obtained from each model were paired-compared by means of covariance analysis (Neter and Wasserman 1974). Comparisons were based on the analysis of the slopes and on the elevations of the different regression lines.

## Results

Linear growth, expressed as a function of initial blade length, is shown for each growth period in Fig. 1. Growth of the blades of *L. longicruris* increased linearly with increasing blade length.

The annual (1980–81) growth pattern of *L. longicruris* in Baie des Chaleurs (L. Gendron, unpubl. data) was similar to that observed in Pubnico, Nova Scotia (Gagné et al. 1982). It was characterized by a peak in June ($2.3\,cm \cdot d^{-1}$) followed by a gradual decrease to a winter minimum ($0.6\,cm \cdot d^{-1}$) and then, beginning in early spring, by a gradual increase to the summer maximum. Growth did not appear to be nitrogen limited, since concentrations of usable nitrogen compounds ($NO_3^-$, $NO_2^-$, $NH_4^+$) in seawater never fell below $4\,\mu mol \cdot L^{-1}$ (L. Gendron, unpubl. data).

This study was carried out in the period following the summer maximum and a regular decrease in growth occurred as the season progressed, as it appears in Fig. 1.

Increases in biomass during the three growth periods estimated using the different models are shown in Fig. 2. Regression parameters describing the linear relationship between biomass increase and initial blade weight are given in Table 2.

Differences between biomass production values obtained using models I and II were not significant (Table 3). Estimates obtained using the chordal model were <10% lower than those obtained using the exponential model (Table 4). Differences between these two models showed a slight diminution as season progressed and linear growth decreased.

Marked differences were, however, obvious between model III and models I and II. The smaller slope of the regression line obtained using model III was significantly different ($P < 0.001$) from the other two (Table 3). Hence, as the blade gets larger, the difference between model III and the two other models becomes greater. Production estimates for small blades (≤50 cm) obtained using model III showed on the average a 7% difference from estimates assessed using model I; for larger blades, the maximum difference was 45% lower (Table 4). Differences between models II and III were similar.

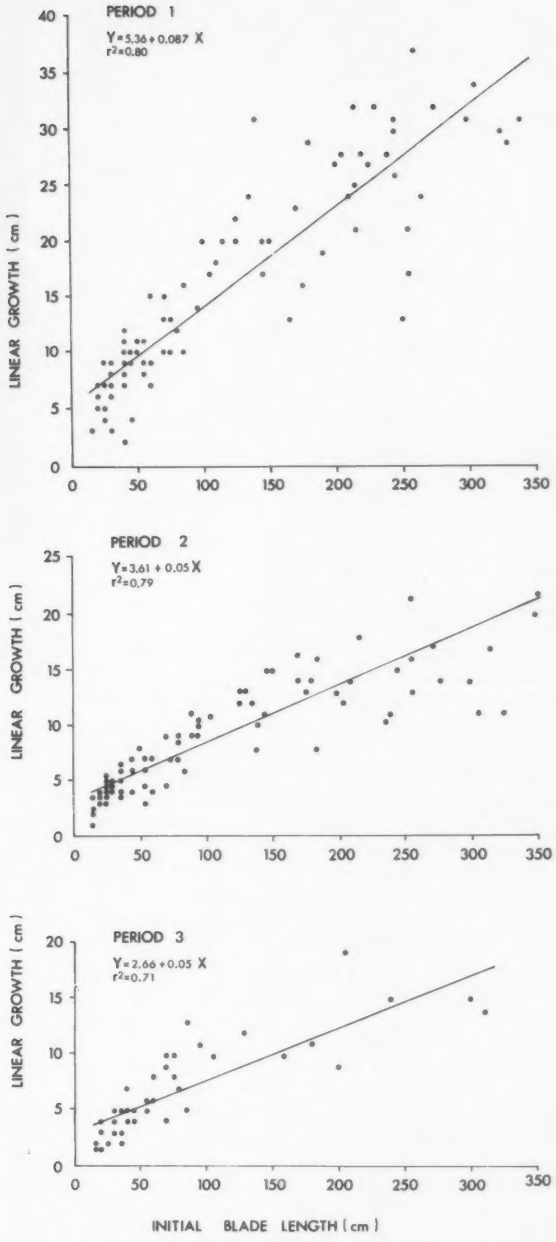


FIG. 1. Linear growth of *L. longicruris* expressed as a function of blade initial length, for each of the three growth periods.

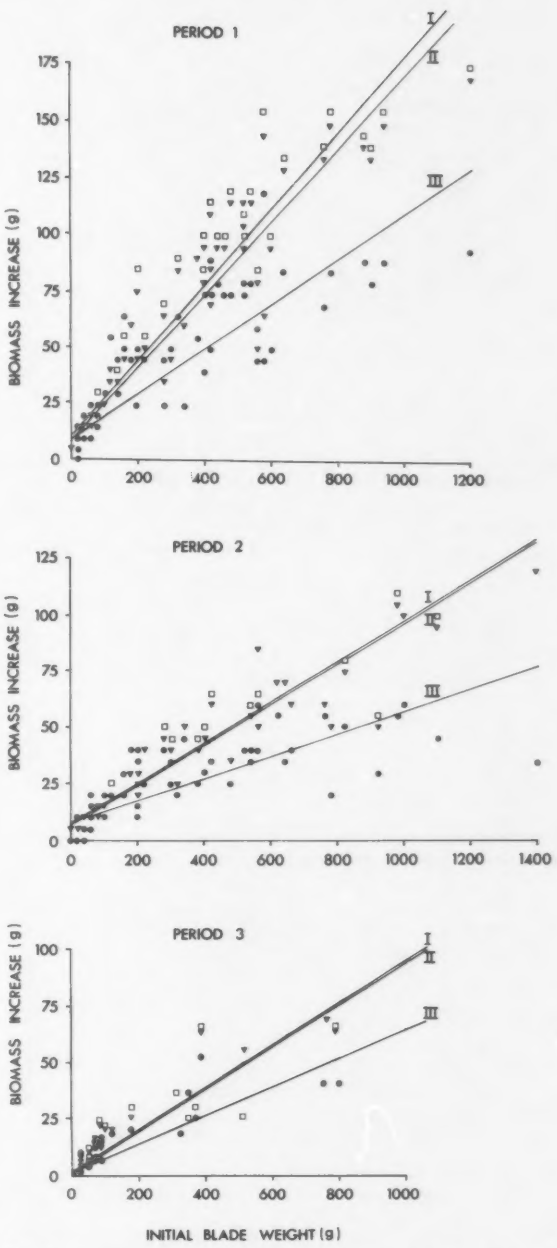


FIG. 2. Increases in biomass of *L. longicruris* expressed as a function of blade initial weight, calculated by the three different models for the three growth periods. □, model I; ▼, model II; ●, model III. Values for regression equations are given in Table 2.

A general curve showing the differences in biomass production estimates between models I and III, expressed as a percentage of model I estimates, is shown in Fig. 3. The differences were similar for the three growth periods.

## Discussion

Production estimates using the three methods varied according to expectations, since models I and II yielded similar results, while estimates from model III were lower than the other two. Biomass production estimates using models I and II differed most during the first growth period, when linear growth was the fastest. Mann and Mann (1981) estimated that the error involved in the calculation of biomass production using model I compared with model II could reach 15% for a 35-cm length increment on a blade 1 m long. The extent of the difference

TABLE 2. Parameters of the linear regression ($Y = a + bX$) of the relationship between biomass increase ($Y$) and initial blade weight ($X$) of *L. longicruris* calculated by the exponential model (I), the chordal model (II), and the biomass model (III) for the three growth periods. Data for calculations are shown in Fig. 2.

| Growth period | Model | $a$ | $b$ | $r^2$ | $n$ |
|---|---|---|---|---|---|
| 22 June – 13 July | I | 9.18 | 0.17 | 0.90 | 91 |
| | II | 8.44 | 0.16 | 0.91 | 91 |
| | III | 10.20 | 0.10 | 0.77 | 91 |
| 14 July – 3 Aug. | I | 5.83 | 0.09 | 0.91 | 93 |
| | II | 5.57 | 0.09 | 0.91 | 93 |
| | III | 7.22 | 0.05 | 0.66 | 93 |
| 3–24 Aug. | I | 4.11 | 0.09 | 0.88 | 45 |
| | II | 3.92 | 0.09 | 0.89 | 45 |
| | III | 4.19 | 0.06 | 0.76 | 45 |

TABLE 3. $F$-values for homogeneity of slopes test and treatment effects test obtained from the covariance analysis performed on the biomass increases in *L. longicruris* expressed as a function of blade initial weight (*$P < 0.001$).

| Models compared | Growth period: 22 June – 13 July | 14 July – 3 Aug. | 3–24 Aug. |
|---|---|---|---|
| | *Homogeneity of slopes test* | | |
| I–II | 0.45 | 0.24 | 0.05 |
| I–III | 64.29* | 76.4* | 25.2* |
| II–III | 58.37* | 73.0* | 24.0* |
| | *Treatment effects test* | | |
| I–II | 0.80 | 0.24 | 0.08 |

TABLE 4. Biomass increase (grams) calculated from the regression equations for different initial blade sizes of *L. longicruris*. Numbers in parentheses are percentages of model I estimates.

| | Initial blade length (cm), initial blade weight (g) | | | | | |
|---|---|---|---|---|---|---|
| Model | 25, 10.7 | 50, 33.7 | 100, 112.1 | 200, 373.3 | 300, 754.4 | 400, 1242.7 |
| Period 1 | | | | | | |
| I | 10.9 | 14.9 | 28.2 | 72.6 | 137.4 | 220.4 |
| II | 10.3 | 13.9 | 26.4 | 68.2 | 129.1 | 207.3 |
| | (94.5) | (93.3) | (93.6) | (93.9) | (94.0) | (94.1) |
| III | 11.2 | 13.6 | 21.4 | 47.5 | 85.6 | 134.5 |
| | (102.8) | (91.3) | (75.9) | (65.4) | (62.3) | (61.0) |
| Period 2 | | | | | | |
| I | 6.8 | 8.9 | 15.9 | 39.4 | 73.7 | 124.7 |
| II | 6.5 | 8.6 | 15.7 | 39.2 | 73.5 | 124.4 |
| | (95.6) | (96.6) | (98.7) | (99.5) | (99.7) | (99.8) |
| III | 7.8 | 8.9 | 12.8 | 25.9 | 44.9 | 69.4 |
| | (114.7) | (100.0) | (80.5) | (65.7) | (60.9) | (55.7) |
| Period 3 | | | | | | |
| I | 5.1 | 7.1 | 14.2 | 37.7 | 72.0 | 123.0 |
| II | 4.9 | 7.0 | 14.0 | 37.5 | 71.8 | 122.8 |
| | (96.1) | (98.6) | (98.6) | (99.5) | (99.7) | (99.9) |
| III | 4.8 | 6.2 | 10.9 | 26.6 | 49.5 | 78.8 |
| | (94.1) | (87.3) | (76.8) | (70.6) | (68.8) | (64.1) |

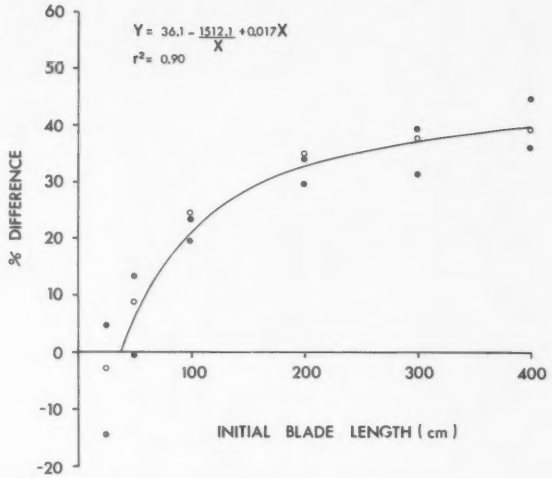


FIG. 3. Differences between model I and model III biomass production estimates expressed as a percentage of model I estimates, in relation to blade initial length. ○, period 1; ⊙, period 2; ●, period 3.

observed between models I and II is a function of linear growth. For small increases in length, the two models give similar results, since in model I, only a small section of the power curve examined is taken into consideration. As the section of the curve examined becomes smaller, the chord by which it can be approximated becomes equivalent to that describing model II. Thus, when small linear growth is converted to biomass production, no substantial differences are to be expected by using model II rather than model I. Although model II has been viewed as an improvement in the conversion of linear increments into biomass production, at least for large length increments, it still overestimates production because it is based on a generalized length to weight relationship that is made inaccurate due to blade erosion.

Model III is independent of such relationships and is not influenced by blade erosion. For this reason, it can be viewed as a more reliable method, providing all meristematic tissue is included in the blade section below the punched hole and providing that the morphology of the plant stays relatively constant during the time interval where growth is measured (Mann and Kirkman 1981). Punching the hole at 20 cm above the stipe and maintaining short time intervals (3 wk) between growth measurements allowed meeting to a significant extent the assumptions necessary for the validity of the biomass model.

Therefore, assuming as mentioned earlier that the biomass model is reasonably accurate, deviations of models I and II from model III can thus be taken as measurements of the error involved in the use of the first two models in production studies. Deviations observed clearly reflect an overestimation of model I and model II biomass production values.

Deviations of models I and II from model III were relatively constant during the three growth periods, and a general correction equation for estimating biomass production using the exponential model was established (Fig. 3). By using this blade size related correction equation with the size frequency distribution of a population, it is therefore possible to assess the error involved in the calculation of biomass production by model I for a whole population.

The correction equation has been derived from summer growth measurements. Whether this equation can be used for correcting estimates of production over an annual cycle depends on the constancy of the length to weight relationship. There is evidence that severe blade erosion during autumn leads to higher $b$ values in the power curve (Gendron 1983), which can cause even higher overestimations of production. The extent to which this could modify the magnitude of the differences that have just been calculated between models I and III was not assessed. However, the effects are probably minor, since in autumn, growth rates are lower, and there are fewer larger plants for which the overestimation is greatest (L. Gendron, unpubl. data).

The advantages and disadvantages of using model III have been discussed by Mann and Kirkman (1981). The calculation of biomass production using the biomass model probably not only results in better estimates but is also more efficient because it requires fewer underwater measurements. However, since the use of this model necessitates that the shape and size of plants stay relatively constant during the time interval where growth is measured, frequency of measurements has to be increased markedly, comparatively to the use of the exponential model.

Model III may be seen as a more reliable method and therefore its use should be favored. However, this study also shows that whether model I or model III is to be used in future studies, it is possible to derive from a correction equation a means for comparing and converting production estimates obtained by either method. The correction equation I generated is itself only applicable to plants of specific morphology, i.e. characteristic of sheltered habitats (Gérard and Mann 1979). However, the procedure for deriving such a correction equation is nevertheless applicable to plants of exposed habitats.

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## References

GAGNÉ, J. A., K. H. MANN, AND A. R. O. CHAPMAN. 1982. Seasonal patterns of growth and storage in *Laminaria longicruris* in relation to differing patterns of availability of nitrogen in the water. Mar. Biol. 69: 91–101.

GENDRON, L. 1983. Inventaire des populations de Laminaires de la Baie des Chaleurs (secteur Caps Noirs – Pointe Bonaventure). Ministère de l'Agriculture, des Pêcheries et de l'Alimentation, Québec. Direction Générale des pêches maritimes. Cahier d'information no. 111: 52 p.

GÉRARD, V. A., AND K. H. MANN. 1979. Growth and production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement. J. Phycol. 14: 319–324.

HATCHER, B. G., A. R. O. CHAPMAN, AND K. H. MANN. 1977. An annual carbon budget for the kelp *Laminaria longicruris*. Mar. Biol. 44: 85–96.

MANN, K. H. 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. Mar. Biol. 14: 199–209.

MANN, K. H., N. JARMAN, AND G. DIECKMAN. 1979. Development of a method for measuring the productivity of the kelp *Ecklonia maxima* (Osbeck) Papenf. Trans. R. Soc. S. Afr. 44: 27–41.

MANN, K. H., AND H. KIRKMAN. 1981. Biomass method for measuring productivity of *Ecklonia radiata*, with the potential for adaptation to other large brown algae. Aust. J. Mar. Freshwater Res. 32: 297–304.

MANN, K. H., AND C. MANN. 1981. Problems of converting linear growth increments of kelps to estimates of biomass production. Xth Int. Seaweed Symp. 699–704.

NETER, J., AND W. WASSERMAN. 1974. Applied linear statistical models. Regression, analysis of variance and experimental designs. Richard D. Irwin, Illinois. 842 p.

PARKE, M. 1948. Studies of the British *Laminariaceae* I. Growth in *Laminaria saccharina* (L.) Lamour. J. Mar. Biol. Assoc. U.K. 27: 651–709.

# Chloroform–Methanol Extraction of Chlorophyll *a*

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Wood, L. W. 1985. Chloroform–methanol extraction of chlorophyll a. Can. J. Fish. Aquat. Sci. 42: 38–43.

Chloroform–methanol (2:1, v/v) extracts significantly more ($P < 0.001$) chlorophyll *a* from algal cultures and from freshwater and seawater microcosms than does dimethyl sulfoxide, methanol, absolute methanol with hydrogen sulfide, or 90% acetone. For chlorophyte cultures it yields 97% or more of the chlorophyll *a* within a 4-h steeping period without grinding. It can be used with both calibrated spectrophotometric and fluorometric instrumentation. Sample filtration onto $MgCO_3$-coated filters is recommended to ensure buffering of the extraction mixture. Holding the filters in chloroform–methanol at 4°C or room temperature in the dark prevents loss of chlorophyll *a* for at least 10 d. More refined analyses of phaeophytin and other chlorophylls require the use of chloroform–methanol–water (2:2:1.8, by volume) and placement in a separatory funnel. After 24 h the lower (chloroform) layer contains all of the chlorophyll. Strict pH control is required for pheophytin determinations.

Pour extraire la chlorophylle *a* de cultures d'algues et de microorganismes d'eau douce et d'eau salée, le chloroforme en mélange avec du méthanol (2 : 1, v/v) est supérieur dans une mesure significative ($P <$ 0,001) au diméthylsulfoxyde, au méthanol, au méthanol absolu en mélange avec de l'acide sulfhydrique et à l'acétone à 90%. Dans le cas des cultures de chlorophytes, on peut extraire au moins 97 % de la chlorophylle *a* par un trempage de 4 h, sans broyage. L'extrait peut être analysé au spectrophotomètre et au fluoromètre après étalonnage. Il est recommandé de le filtrer sur filtres à revêtement de $MgCO_3$ pour le tamponner. En gardant les filtres à l'obscurité dans un mélange de chloroforme et de méthanol à 4°C ou à la température de la pièce, on peut conserver la chlorophylle *a* au moins 10 jours. Pour analyser la phaeophytine et d'autres types de chlorophylle de façon plus poussée, on doit utiliser un mélange de chloroforme, de méthanol et d'eau (2 : 2 : 1,8, en volume) et placer la solution dans un entonnoir à séparation ; au bout de 24 h, toute la chlorophylle est descendue dans la couche inférieure (chloroforme). Pour le dosage de la phéophytine, le pH doit être étroitement surveillé.

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Problems have often been observed in extracting chlorophyll *a* with 90% acetone (APHA 1976; UNESCO 1966; Strickland and Parsons 1968; Vollenweider 1969; Rai 1980). After centrifugation, the $MgCO_3$ pellet commonly contains greenish materials, which indicates incomplete extraction. Incomplete removal of chlorophyll from phytoplankton samples increases the variance associated with empirical models relating phosphorus or nutrient loadings to this substance (Vollenweider 1976). Less than accurate estimates of chlorophyll also compromise estimates of planktonic algal biomass and impair monitoring of the quality of potable or other surface waters (Jones and Lee 1982).

These concerns prompted a search for a more efficient extractant or extraction procedure. A chloroform–methanol mixture (C–M; 2:1, v/v) commonly used in lipid research was tested, along with other extractants, to determine its usefulness for quantitation of chlorophyll in phytoplankton samples.

## Methods

On the basis of preliminary experiments, five promising extractants were selected for comparative testing with a variety of algal cultures. The five were 90% acetone, absolute methanol (Marker 1972), dimethyl sulfoxide ($Me_2SO$; Shoaf and Lium 1976, 1977), methanol saturated with hydrogen sulfide (S–M; Holm-Hanson and Riemann 1978; Jenson and Sakshaug 1973), and C–M (Folch et al. 1957). Other extractants tested in the preliminary experiments were *N*,*N*-dimethyl foramide (Belly et al. 1973), pyridine (T. T. Bannister, University of Rochester, Rochester, NY, pers. comm.), tetra- and tri-chloroethylene, chloroform, ether, and ethanol.

The cultures, maintained by G-Y. Rhee, New York State Health Department, included chlorophytes, chrysophytes, and cyanophytes, three major divisions of the phytoplankton. These cultures were grown in appropriate media and diluted just prior to filtration. In addition, phytoplankters from laboratory-grown saltwater and freshwater microcosms were used. These microcosms, derived from initial inocula of water and sediment, had been maintained for at least 1 yr under a 12 h light : 12 h dark cycle at room temperature (23°C).

Field samples were collected by the hose integration technique (Dillon and Rigler 1974) or by mixing the Van Dorn sampler contents from selected depths to represent the water stratum under consideration. Each sample was stored a maximum of 2 h in a plastic bottle in the dark before processing.

Both field and laboratory filtrations used 0.45-μm Millipore filters (2.5-cm diameter for fluorometry, 4.5-cm for spectrophotometry) coated with 1 or 5 mL of a $MgCO_3$ suspension

(5 $g \cdot L^{-1}$). Glass-fiber filters are less efficient, as they allow algal cells to pass through (Munawar et al. 1982; Rai 1980; Lenz and Fritsche 1980), and were used only when Teflon/glass tissue maceration was required. The field samples (10–50 mL for fluorometry, usually 250 mL for spectrophotometry) were passed through at ≤9 cmHg vacuum. Each filter was then rolled and placed in a screw-capped centrifuge tube, and 10 mL of extractant was added. The tubes were placed in light-tight containers and transported to the laboratory on dry ice. In a recent modification the tubes were maintained at ambient temperature during transport so that some extraction could occur.

In the laboratory all tubes were vortexed under subdued light, stored in the dark for at least 4 h, and then centrifuged at 1500 rpm. For fluorometric determinations of chlorophyll we used a Turner model 111 fluorometer equipped with a red-sensitive photomultiplier, a blue lamp, a primary filter (maximum transmission 430 nm), and a secondary filter (allowing passage of wavelengths greater than 650 nm). For spectrophotometry we used a Bausch & Lomb 505 recording spectrophotometer with 5-cm cells, scanning 600–700 nm. Both instruments were calibrated with known stock solutions prepared from freshly obtained chlorophyll *a* (Sigma Chemical Co.; see Grantham 1981). The commercial product was first passed through a powdered sugar chromatography column and then diluted with the extractant under study to obtain standard curves.

Chromatography of the commercial chlorophyll on powdered sugar produced one band. It had an extinction ratio (428/662 nm) in diethyl ether of 1.27–1.33, which brackets the reported values of 1.30 (Strain et al. 1963) and 1.31 (Seely and Jensen 1965). The molar extinction ratio ($\times 10^4$ L/mol-cm) in diethyl ether was 8.43 ± 0.12 (mean ± SD), near the reported values of 8.51 (Seely and Jensen 1965) and 8.63 (Strain et al. 1963) but below the values of 9.12 (Zscheile and Comar 1941) and 9.01 (Smith and Benitz 1955) obtained in ether for the red band. Molar extinction ratios in other solvents were 652 ± 0.54 in methanol, 7.26 ± 0.97 in 90% acetone, 6.94 ± 0.52 in $Me_2SO$, and 7.05 ± 0.21 in chloroform. All means were lower than those reported by Seely and Jensen (1965) but were, except for acetone, within 1 SD of their values. Only the 90% acetone coefficient was outside the 1 SD range for the published value for 100% acetone, but it was within 1 SD of the Jeffrey and Humphrey (1975) mean for 90% acetone. In C–M the molar extinction coefficient was 6.74 ± 0.16.

The time required to extract chlorophyll with C–M was determined with a *Scenedesmus* culture.This alga was one of the more difficult phytoplankters to extract. Four filters were extracted each hour for 8 h after filtration.

To check for efficiency of extraction a dense 1400-mL culture of *Selenastrum* was extracted for 4 h and then passed through a glass-fiber filter. This filter, which contained $MgCO_3$ and algal remains, was extracted for residual chlorophyll by a procedure that included Teflon/glass grinding of tissue in C–M extractant.

Laboratory tests to validate field procedures were done with a *Scenedesmus* culture. This culture was diluted, and portions were filtered through 38 filters. Each day for 10 d, four filters in their tubes were removed from a freezer (−20°C) or from a cabinet at room temperature (23°C) for C–M extraction and chlorophyll determination. All tubes were maintained in light-tight boxes.

Additional tests of storage in the extractant, rather than as moist filters, were performed to test the effect of C–M on chlorophyll stability. All storage at freezer or room temperature was done in light-tight containers.

The possibility that methanol may be quenching fluorescence in our determinations of chlorophyll *a* was investigated with a 10-mL acetone extract of an *Anabaena* culture. This extract was divided into 5-mL portions, one of which received a series of 200-μL additions of acetone, and the other a series of 200-μL additions of methanol. Loss of fluorescence was determined after each addition.

I used analysis of variance and the Student's *t*-test to detect significant differences among treatments.

## Results and Discussion

### Effectiveness of Extractants

For chlorophycean cultures, C–M was clearly the most efficient extractant (Table 1). Significant differences in effectiveness between C–M and acetone or S–M were found with both *Scenedesmus* and *Selenastrum*. As reported by Holm-Hansen and Riemann (1978), S–M extracted significantly more chlorophyll than did acetone from *Selenastrum*, but it extracted significantly less than C–M.

Diatom and chyanophycean cultures showed smaller differences among these three extractants, but again C–M was consistently the most efficient. In contrast with the chlorophycean cultures, S–M tended to extract the least amount of chlorophyll *a*. For *Anacystis* the mean was higher (but not statistically so) with acetone than with C–M.

With a saltwater microcosm (salinity about 32‰) composed mostly of a chlorophyte (possibly *Nannochloris* sp.) and a diatom (*Cyclotella* sp.), C–M extracted significantly more chlorophyll *a* than did acetone or S–M. Similar results were obtained with a freshwater microcosm containing mostly *Botryococcus brauni* but also *Oedogonium* and an unidentified chlorophyte. Other phytoplankters not numerous enough for quantification included *Navicula*, *Oscillatoria*, *Tetrahedron*, *Cryptomonas*, *Chroococcus*, and *Anacystis*.

Comparative extractions to confirm these results were done with C–M, acetone, and $Me_2SO$ on 11 other algal cultures: Chlorophyta: *Selenastrum capricornutum*, *Scenedesmus* sp., *Oocystis* sp., *Chlamydomonas* sp., and *Ankistrodesmus* sp.; Chrysophyta: *Fragilaria brevistriata*, *Asterionella formosa*, and *Nitzschia* sp.; and Cyanophyta: *Oscillatoria* sp., *Anabaena flos-aquae*, and *Anacystis incerta*. These results (data not shown) confirmed that C–M is equal or superior to the other extractants. Ten of the 11 cultures yielded significantly more chlorophyll *a* with C–M (8 at $P = 0.001$ and 2 at $P = 0.05$). Only one culture (*Fragilaria brevistriata*) showed equal extraction efficiencies. Traces of green, often observed in acetone and $Me_2SO$ centrifuge pellets, were absent with C–M, and the chlorophyll remaining in the acetone and $Me_2SO$ pellets could be extracted with C–M. From a *Scenedesmus* culture, for example, acetone with Teflon/glass grinding extracted 11.04 $\mu g \cdot L^{-1}$. Extraction of the centrifugate with C–M yielded an additional 10.7 $\mu g \cdot L^{-1}$, and extraction of a duplicate sample with C–M alone yielded 26.96 $\mu g \cdot L^{-1}$.

In a third set of experiments methanol was used as well as C–M, S–M, and acetone with three algal species and the seawater microcosm (Table 1). Again the superiority of C–M was confirmed. Absolute methanol and 90% acetone extracted chlorophyll *a* from *Asterionella* with equal efficiency, as has been noted by other authors (Holm-Hanson and Riemann 1978;

TABLE 1. Comparative extraction by C–M, 90% acetone, methanol (100%), and S–M of chlorophyll *a* from algal cultures and microcosm samples. $N = 12$ (or 4 for those with methanol) for each experiment. $P$ = probability level from analysis of variance with $F_{2,33}$ degrees of freedom ($F_{3,12}$ for experiments containing methanol). $P$ represents comparisons with C–M results.

| Class and genus | Extractant | Mean (SD) ($\mu g \cdot L^{-1}$) | | $P$ |
|---|---|---|---|---|
| Chlorophyta | | | | |
| *Selenastrum* | C–M | 131.6 | (1.7) | |
| | Acetone | 35.7 | (10.0) | <0.001 |
| | S–M | 91.5 | (10.6) | |
| *Scenedesmus* | C–M | 27.6 | (1.2) | |
| | Acetone | 0.9 | (0.1) | <0.001 |
| | S–M | 1.3 | (0.2) | |
| *Chalamydomonas* | C–M | 182.6 | (22.4) | |
| | Acetone | 103.5 | (44.4) | |
| | S–M | 49.2 | (10.0) | <0.001 |
| | Methanol | 63.0 | (16.8) | |
| Chrysophyta | | | | |
| *Fragilaria* | C–M | 1.5 | (0.1) | |
| | Acetone | 1.5 | (0.1) | <0.001 |
| | S–M | 1.2 | (0.1) | |
| *Asterionella* | C–M | 2.1 | (0.1) | |
| | Acetone | 1.5 | (0.5) | <0.001 |
| | S–M | 1.4 | (0.2) | |
| *Asterionella formosa* | C–M | 49.2 | (13.5) | |
| | Acetone | 27.6 | (10.1) | |
| | S–M | 14.6 | (8.1) | <0.001 |
| | Methanol | 26.4 | (5.1) | |
| Cyanophyta | | | | |
| *Oscillatoria* | C–M | 3.0 | (0.4) | |
| | Acetone | 1.5 | (0.6) | <0.001 |
| | S–M | 2.2 | (0.2) | |
| *Anabaena* | C–M | 83.3 | (5.5) | |
| | Acetone | 72.7 | (9.9) | <0.001 |
| | S–M | 55.0 | (8.8) | |
| *Anacystis* | C–M | 24.8 | (0.5) | |
| | Acetone | 26.3 | (2.7) | <0.001 |
| | S–M | 17.2 | (2.5) | |
| *Anacystis incerta* | C–M | 107.2 | (4.8) | |
| | Acetone | 42.3 | (5.8) | |
| | S–M | 25.1 | (4.2) | <0.001 |
| | Methanol | 54.3 | (10.4) | |
| Microcosm | | | | |
| Saltwater | C–M | 86.5 | (1.5) | |
| | Acetone | 12.1 | (2.8) | <0.001 |
| | S–M | 63.0 | (5.1) | |
| Saltwater | C–M | 342.7 | (8.8) | |
| | Acetone | 8.1 | (6.1) | |
| | S–M | 95.1 | (55.4) | <0.001 |
| | Methanol | 69.9 | (18.5) | |
| Freshwater | C–M | 50.6 | (1.8) | |
| | Acetone | 17.5 | (1.8) | <0.001 |
| | S–M | 37.7 | (1.1) | |

Talling and Driver 1961), but neither was as efficient as C–M. Thus, even diatoms may not always be extracted completely by the solvents in common use.

Except from the seawater microcosm, absolute methanol extracted consistently more chlorophyll *a* than did S–M. Acetone was superior to the two methanol extractants for *Chlamydomonas*, intermediate between methanol and S–M for *Anacystis*, equal to methanol for *Asterionella*, and by far the poorest for the saltwater microcosm.

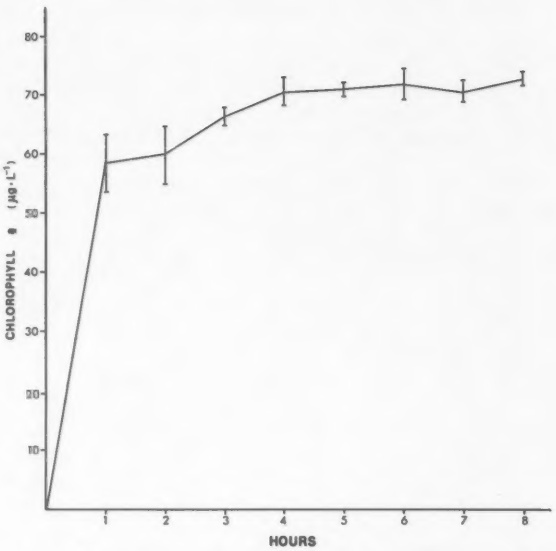


FIG. 1. Extraction of chlorophyll *a* from a *Scenedesmus* culture by C–M at various time intervals. Vertical bars represent ±1 SD ($N = 4$).

TABLE 2. Effect of freezing of filters on extraction by 90% acetone, $Me_2SO$, and C–M of chlorophyll from unialgal cultures. Chlorophyll values are mean (SD); $N = 4$ for each experiment. NS = not significant at $P < 0.05$ (Students' $t$-test).

| Species and parameter | Extractant | | | | | |
|---|---|---|---|---|---|---|
| | Acetone | | $Me_2SO$ | | C–M | |
| *Anacystis incerta* | | | | | | |
| Unfrozen | 4.6 | (0.3) | 77.4 | (7.0) | 76.1 | (3.3) |
| Frozen | 2.2 | (0.2) | 16.9 | (2.2) | 74.4 | (2.2) |
| Loss (%) | 52.1 | | 78.1 | | 2.2 | |
| $P$ | <0.001 | | <0.001 | | NS | |
| *Nitzschia* sp. | | | | | | |
| Unfrozen | 39.0 | (0.5) | 37.1 | (1.3) | 49.5 | (6.4) |
| Frozen | 13.2 | (0.3) | 14.0 | (1.5) | 46.0 | (1.6) |
| Loss (%) | 66.1 | | 62.2 | | 7.2 | |
| $P$ | <0.001 | | <0.001 | | NS | |

The minimal time required to extract chlorophyll with C–M, as determined from a culture of *Scenedesmus*, was 4 h. Significant differences in extraction were found between time periods up to 4 h but not thereafter (Fig. 1).

Extraction of a *Selenastrum* culture with C–M for 4 h yielded 1.84 $mg \cdot L^{-1}$. No chlorophyll could be obtained from the residue on the glass-fiber filter by grinding and C–M extraction of the algal remains. Thus, chlorophyll *a* had been completely extracted within the 4-h steeping period from this dense culture of the alga, in agreement with the *Scenedesmus* results.

## Effect of Storage Time, Temperature, and Filter Preparation

Samples collected from lakes and streams for chlorophyll determination must often be filtered in the field and stored for analysis at a future time. Commonly the samples are processed and the filters, with $MgCO_3$ and particulate materials, are maintained in the dark in a freezer or on dry ice during transport.

TABLE 3. Effect of filter treatment (water, $MgCO_3$, or Celite) on extraction with C–M, 90% acetone, or S–M. Chlorophyll values are mean (SD); $N = 4$ for each treatment and extractant ($F_{2,9}$). NS = not significant.

| Organism | Extractant | Mean (SD) ($\mu g \cdot L^{-1}$) | | | |
|---|---|---|---|---|---|
| | | Water[a] | $MgCO_3$ | Celite[b] | $P$ |
| *Selenastrum* | C–M | 130.48 (1.54) | 131.56 (1.06) | 132.94 (1.76) | NS |
| | Acetone | 82.80 (3.97) | 33.12 (11.73) | 42.78 (9.43) | NS |
| | S–M | 82.80 (3.97) | 98.90 (13.47) | 92.92 (6.10) | NS |
| *Scenedesmus* | C–M | 28.76 (0.32) | 26.65 (0.70) | 27.30 (1.06) | <0.05 |
| | Acetone | 0.79 (0.11) | 1.00 (0.13) | 0.87 (0.03) | <0.05 |
| | S–M | 1.22 (0.07) | 1.59 (0.12) | 1.30 (0.14) | <0.001 |
| *Fragilaria* | C–M | 1.59 (0.07) | 1.63 (0.07) | 1.42 (0.03) | <0.01 |
| | Acetone | 1.62 (0.08) | 1.39 (0.13) | 1.59 (0.08) | <0.05 |
| | S–M | 1.17 (0.03) | 1.39 (0.03) | 1.09 (0.03) | <0.001 |
| *Asterionella* | C–M | 2.08 (0.13) | 2.10 (0.05) | 2.10 (0.10) | NS |
| | Acetone | 1.38 (0.15) | 1.44 (0.44) | 1.80 (0.64) | NS |
| | S–M | 1.21 (0.12) | 1.59 (0.11) | 1.48 (0.03) | <0.001 |
| *Anabaena* | C–M | 86.02 (8.00) | 81.42 (4.08) | 82.34 (4.08) | NS |
| | Acetone | 65.78 (5.49) | 80.50 (8.14) | 71.76 (10.96) | NS |
| | S–M | 48.30 (2.76) | 65.80 (4.33) | 51.06 (4.84) | <0.001 |
| *Oscillatoria* | C–M | 2.89 (0.43) | 3.24 (0.22) | 2.79 (0.30) | NS |
| | Acetone | 1.54 (0.28) | 2.23 (0.74) | 2.65 (0.29) | <0.05 |
| | S–M | 2.02 (0.54) | 2.55 (0.19) | 2.04 (0.08) | NS |
| *Anacystis* | C–M | 25.19 (0.62) | 24.70 (0.00) | 24.54 (0.32) | NS |
| | Acetone | 25.35 (4.60) | 27.14 (0.82) | 26.49 (1.62) | NS |
| | S–M | 15.76 (0.67) | 20.47 (0.65) | 15.44 (0.32) | <0.001 |
| Microcosm | | | | | |
| Freshwater | C–M | 51.06 (1.76) | 50.60 (1.84) | 48.76 (1.06) | NS |
| | Acetone | 16.41 (1.71) | 17.55 (1.76) | 16.25 (1.30) | NS |
| | S–M | 31.36 (2.62) | 35.75 (1.06) | 35.11 (0.90) | <0.05 |
| Saltwater | C–M | 88.32 (2.12) | 86.48 (1.90) | 86.48 (2.60) | NS |
| | Acetone | 9.90 (2.13) | 12.10 (2.77) | 7.75 (0.85) | <0.05 |
| | S–M | 63.94 (2.76) | 63.02 (5.07) | 67.62 (1.76) | <0.05 |

[a]Distilled water.
[b]For Celite, 1 mL of a 5 $g \cdot L^{-1}$ suspension was used.

This and alternative procedures were tested for their effect on extraction with C–M.

Storage in C–M enhanced the stability of filters collected in the field. In three of four experiments with *Anabaena* or *Scenedesmus* cultures, no change in chlorophyll concentrations was observed for up to 10 d after addition of C–M, while the extracts were maintained at room temperature in the dark. Dry filters similarly maintained without C–M showed 10-d declines in chlorophyll content, e.g. from 3.04 to 2.4 $\mu g \cdot L^{-1}$ in one experiment and from 117 to 104 $\mu g \cdot L^{-1}$ in another. At refrigerator or freezer temperatures, filters stored in C–M or dry showed no significant changes over periods up to 10 d. Even so, storage time should be minimized as recommended by Marker et al. (1980).

Freezing decreased the ability of acetone and $Me_2SO$ but not C–M to extract chlorophyll *a* (Table 2). Filters stored frozen for 24 h without extractant yielded 52% less chlorophyll when extracted with acetone and 78% less when extracted with $Me_2SO$ than filters kept at room temperature. Similar freezer storage problems have been related to the water content of the filters and/or entrapment in $MgCO_3$ aggregates (Nusch 1980). In contrast, decreases in the efficiency of C–M-extracted filters were not statistically significant. F. P. Healey (Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Man. R3T 2N6, pers. comm.) reports no freezing effects for extraction from *Anabaena* or *Scenedesmus* with methanol. The magnitude of any freezing effect may thus be related to the species of alga being extracted and the choice of water or $MgCO_3$ for filter treatment, as well as the extractant's efficiency.

A requirement for $MgCO_3$ as a buffer was shown in tests of S–M, C–M, and acetone with seven algal cultures and the two microcosms. $MgGO_3$ treatment was needed for two of the nine chlorophyll sources with C–M, for four with acetone, and for five with S–M (Table 3).

Dilution with methanol caused a more rapid decrease in fluorescence than did dilution with acetone, suggesting that methanol does act as a quencher. The C–M results after 5, 15, and 25% dilutions were 0.1, 1.3, and 2.3 fluorescence units lower than the acetone results. Consequently, care should be taken to maintain consistency between the C–M mixtures used for calibration and for sample extraction.

## Spectrophotometric Considerations

Portions of an *Anabaena* culture extracted with C–M and acetone (four replicates per treatment) showed similar amounts

of chlorophyll when determined spectrophotometrically (means 14.30 and 14.13 $\mu g \cdot L^{-1}$, respectively). However, when samples were acidified with acetic acid for phaeophytin determinations, significantly more phaeophytin *a* was found in the acetone than in the C–M extracts (0.97 vs. 1.06 $\mu g \cdot L^{-1}$; $P < 0.05$).

With C–M the addition of HC1, which normally has a large water component, for phaeophytin determinations causes polar–nonpolar turbidity. This problem was solved by using concentrated acetic acid and a microlitre pipette to produce the desired acidity without turbidity.

An absorption peak at 665 nm for chlorophyll *a* in C–M extracts was the same as in methanolic extracts (Marker 1972; Holm-Hanson and Riemann 1978). Addition of acid to these extractants can cause formation of the dication form of phaeophytin *a*, with an absorbance peak at 655 nm (Usacheva 1971). This region is also the peak for chlorophyll *b* (655 nm) and pheophytin *b* (653 nm), so pheophytin *a* cannot be determined in the presence of chlorophyll *b* or pheophytin *b* by simple acidification. Attempts to solve this problem have often involved removing the methanol and redissolving the pigments in another solvent (Marker 1972).

With C–M the pigments can be isolated into the chloroform phase by adding water to a ratio of 2:2:1.8 (chloroform–methanol–water). A phase separation then occurs in a separatory funnel over a 24-h period: the aqueous phase contains the methanol and the chloroform phase the chlorophyll and phaeopigments. For one sample containing 18.4 mg chlorophyll$\cdot L^{-1}$, all of the chlorophyll was found in the chloroform phase and none in the aqueous methanol phase. Still, the problems with spectral overlap found with other extractants (Rai 1980) remain using chloroform alone.

After extraction by chloroform alone the absorption spectra match those of acetone or $Me_2SO$ extracts (Shoaf and Lium 1976, 1977), allowing analysis of pigment ratios. However, acidification can have rather large effects on the absorption and emission spectra (Moed and Hallegraeff 1978; Usacheva 1971). For all of the studies reported here we strived to keep an apparent pH of 2.6–2.8 (Moed and Hallegraff 1978).

### Effect of C–M on Estimates of Biomass

Relationships between chlorophyll *a* and biomass (Steel and Baird 1965; Holm-Hanson 1969; Eppley 1968; Lorenzen 1968) calculated from acetone extractions of marine samples have varied from station to station, depth to depth, and day to day. Presumably, differences exist among marine phytoplankton similar to those among the freshwater forms studied here. If so, the variance among chlorophyll biomass ratios in marine studies could be related in part to the varying amounts of chlorophyll extracted from the phytoplankton communities sampled.

In field trials with natural phytoplankton assemblages from several lake systems, C–M was superior as an extractant to acetone with tissue grinding. In 43 paired determinations from Belmont Lake, Long Island, NY, for example, 29 (67%) showed higher chlorophyll values with C–M, whereas 11 (26%) showed higher values with acetone (unpublished data). The remaining pairs gave identical values. The C–M values exceeded acetone values by up to 31 $\mu g \cdot L^{-1}$ (actual values: 66.6–35.6), while acetone values exceeded C–M values by no more than 14.7 $\mu g \cdot L^{-1}$ (actual values: 196.0–181.3). For three sets of quadruplicate samples, two extracted with C–M and two with acetone, one set narrowly favored acetone (means 4.15 vs. 4.05), while two sharply favored C–M (means 7.80 vs. 7.35 and 7.10 vs. 5.45).

From this limited sampling, C–M appears to yield higher chlorophyll results for natural communities much more often than does acetone. However, more extensive studies are needed, and use of C–M data in empirically derived models (Smith 1982; Vollenweider 1976; Vollenweider and Kerkes 1980; Rast and Lee 1978; and others) should be approached with caution.

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## References

AMERICAN PUBLIC HEALTH ASSOCIATION (APHA). 1976. Standard methods for the examination of water and wastewater. 14th ed. APHA, Washington, DC 1193 p.

BELLY, R. T., M. R. TANSEY, AND T. D. BROCK. 1973. Algal excretion of $^{14}C$-labeled compounds and microbial interactions in *Cyanidium caldarium* mats. J. Phycol. 9: 123–127.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19:767–773.

EPPLEY, R. W. 1968. An incubation method for estimating the carbon content of phytoplankton in natural samples. Limnol. Oceanogr. 13: 574–582.

FOLCH, J., M. LEES, AND G. H. S. STANLEY. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226: 497–509.

GRANTHAM, B. 1981. The Loch Eil project: chlorophyll *a* and nutrients in the water column of Loch Eil. J. Exp. Mar. Biol. Ecol. 55: 283–297.

HOLM-HANSON, O. 1969. Determination of microbial biomass in ocean profiles. Limnol. Oceanogr. 14: 740–747.

HOLM-HANSON, O., AND B. RIEMANN. 1978. Chlorophyll *a* determination: improvements in methodology. Oikos 30: 438–447.

JEFFREY, S. W., AND G. F. HUMPHREY. 1975. New spectrometric equations for determining chlorophylls $a$,$b$,$c_1$ and $c_2$ in higher plants, algae and natural phytoplankton. Biochem. Physiol. Pflanzen. (BPP) 167: 191–194.

JENSEN, A., AND E. SAKSHAUG. 1973. Studies on the phytoplankton ecology of the Trondheimsfjord. II. Chlorophase pigments in relation to abundance and physiological state of the phytoplankton. J. Exp. Biol. Ecol. 11: 137–155.

JONES, R. A., AND G. F. LEE. 1982. Chlorophyll — a raw water quality parameter. J. Am. Water Works Assoc. 74: 490–494.

LENZ, J., AND P. FRITSCHE. 1980. The estimation of chlorophyll *a* in water samples: a comparative study on retention in a glass-fibre and membrane filter and on the reliability of two storage methods. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14: 91–106.

LORENZEN, C. J. 1968. Carbon/chlorophyll relationships in an upwelling area. Limnol. Oceanogr. 13: 202–204.

MARKER, A. F. H. 1972. The use of acetone and methanol in the estimation of chlorophyll in the presence of phaeophytin. Freshwater Biol. 2: 361–385.

MARKER, A. F. H., E. A. NUSCH, H. RAI, AND B. RIEMAN. 1980. The measurement of photosynthetic pigments in freshwaters and standardizations of methods: conclusions and recommendations. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14: 91–106.

MOED, J. R., AND G. M. HALLEGRAEFF. 1978. Some problems in the estimation of chlorophyll *a* and phaeo pigments from pre- and postacidification spectrophotometric measurements. Int. Rev. Gesamten Hydrobiol. 63: 787–800.

MUNAWAR, M., I. F. MUNAWAR, P. E. ROSS, AND A. DAGENAIS. 1982. Microscopic evidence of phytoplankton passing through glass fiber filters and its implication for chlorophyll analysis. Arch. Hydrobiol. 94: 520–528.

NUSCH, E. A. 1980. Comparison of different methods for chlorophyll and phaeopigment determination. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14: 14–36.

RAI, H. 1980. Some problems in determination of photosynthetic plankton

pigments and their decomposition products. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14: 3–13.

RAST, W., AND G. F. LEE. 1978. Summary analysis of the North American project: nutrient loading – lake response relationships and trophic state indicies. U.S. EPA-600/3-78-008, Ecol. Res. Ser., Corvallis, OR. 455 p.

SEELY, G. R., AND R. G. JENSEN. 1965. Effect of solvent on the spectrum of chlorophyll. Spectrachim. Acta 21: 1835–1845.

SHOAF, F. T., AND B. W. LIUM. 1976. Improved extraction of chlorophyll *a* and *b* from algae using dimethyl sulfoxide. Limnol. Oceanogr. 21: 926–928.

1977. The quantitative determination of chlorophyll *a* and *b* from freshwater algae without interference from degradation products. J. Res. U.S. Geol. Surv. 5: 263–264.

SMITH, J. H. C., AND A. BENITZ. 1955. Chlorophylls: analysis in plant materials, p. 142–196. *In* K. Paech [ed.] Modern methods of plant analysis. Springer-Verlag, Berlin.

SMITH, V. H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: an empirical and theoretical analysis. Limnol. Oceanogr. 27: 1101–1112.

Steel, J. H., and I. E. Baird. 1965. The chlorophyll *a* content of particulate organic matter in the northern North Sea. Limnol. Oceanogr. 10: 261–267.

STRAIN, H. H., M. R. THOMAS, AND J. J. KATZ. 1963. Spectral absorption properties of ordinary and fully deuterated chlorophylls *a* and *b*. Biochem. Biophys. Acta 75: 306–311.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167: 293 p.

TALLING, J. F., AND D. DRIVER. 1961. Some problems in the estimation of chlorophyll *a* in phytoplankton, p. 142–146. *In* M. S. Doty [ed.] Proc. conf. on Primary Productivity, Marine and Freshwater, Honalake U.S. Atomic Energy Commission, Washington, DC.

UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION (UNESCO). 1966. Determination of photosynthetic figments in seawater. UNESCO Publications Center, Paris. 69 pp. (Monogr. Oceanogr. Methodol.)

USACHEVA, M. N. 1971. Nature of the effect of addition of acids on the spectra and photonics of the molecules of pheophytin. Biophysics 16: 1021–1029.

VOLLENWEIDER, R. A. 1969. Sampling techniques and methods of estimating quantity and quality of biomass. *In* R. A. Vollenweider [ed.] A manual on methods for measuring primary production in aquatic environments. International Biological Programme Handbook No. 12, Blackwell Scientific Publications, Oxford and Edinburgh. 213 p.

1976. Advanced in defining critical loading levels in lake eutrophication. Mem. Ist Ital. Idrobiol. 33: 53–83.

VOLLENWEIDER, R. A., AND J. KERKES. 1980. The loading concept as basis for controlling eutrophication philosophy and preliminary results of the OECD programme on eutrophication. Prog. Water Technol. 12: 5–38.

ZSCHEILE, F. P., AND C. L. COMAR. 1941. Influence of preparative procedure on the purity of chlorophyll components as shown by absorption spectra. Bot. Gaz. 102: 463–481.

# Generalizing Fisheries Models: An Extension of the Schaefer Analysis

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Central to fish harvesting management plans are population estimates and productivity relationships. The conventional Schaefer model, consisting of a fish harvesting production function and a population dynamics equation, is generalized to permit estimation of an unconstrained Cobb–Douglas production function for a fishery in the absence of population data. The generalization results in equilibrium catch and population figures that can be substantially different from conventional Schaefer estimates. The choice of model, therefore, may strongly affect steady-state quota allocations and total allowable catch paths to the steady state.

La planification des pêches repose essentiellement sur les estimations de populations de poissons et l'étude des relations mettant en jeu leur productivité. Le modèle de Schaefer se compose d'une fonction représentant la production pour la pêche et d'une équation représentant la dynamique des populations. Nous avons généralisé ce modèle classique pour estimer la fonction de production sans restriction de Cobb–Douglas sans données sur la population. Les chiffres ainsi obtenus sur la population et la prise d'équilibre peuvent être très différents des estimations obtenues par le modèle Schaefer. La choix du modèle peut donc considérablement influer sur les quotas d'équilibre alloués et sur la prise totale acceptable qui permet d'assurer cet équilibre.

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For nearly 30 yr, the economics literature concerning production functions for fisheries has been dominated by the Schaefer model (Schaefer 1954, 1957). For a perspective on the role of this model in fisheries economics, see Clark (1976), Anderson (1977), and Hannesson (1983). For recent papers utilizing the model, see Stocker and Hilborn (1981) and Kim (1983). The Schaefer model features a primitive Cobb–Douglas production function in which catch is a function of fishing effort and fish population, both exponents assumed to be one, the only estimated parameter being a "catchability coefficient." Fishing effort is an index reflecting the use of labor and capital in combination. Population estimates are often weak or nonexistent. Schaefer handled the problem of nonexistent population figures by developing an iterative technique involving the simultaneous estimation of the production function and a Pearl–Verhulst logistics population function, where the logistics function is a form of dynamic population growth relation often used as a first approximation by biologists. A number of alternative production/population models used in fisheries management are described in Goh (1980).

In this paper, we develop a method for estimating the Schaefer model without restricting the allowable values of the Cobb–Douglas exponents. Hannesson (1983, p. 968–969) noted how restrictive the Schaefer model is, choosing, as do we, to experiment with a logical extension of Schaefer's production function, an extension to a form widely used in economics. Hannesson's approach to the problem was, however, far different from that presented here both in the method used to aggregate fishing effort and, more important, in that Hannesson used biologists' population figures while we continue with Schaefer's assumption that population figures are virtually unavailable. We return to both of these topics later in the paper.

Our technique is not based on the assumption that the Schaefer model is incorrect; it merely provides a method for statistically testing the validity of the Schaefer assumptions and for permitting the estimation procedure to assign values to the exponents, rather than having the researcher assign them by assumption.

The goal of the analysis is to devise improved policy tools. For instance, as a by-product of the main analysis, our technique generates population estimates that may be of higher quality than those generated by cohort analysis. In such cases, the technique discussed here is of use in stock assessment and in the setting of quotas. Of primary interest to the authors, however, is the fact that the model provides a generalized, nonlinear relationship between catch and effort. In a large econometric model of the Newfoundland groundfishery (Schrank et al. 1984), the authors obtained generalized Schaefer estimates for nine fish stocks and embedded these estimates in a broad framework of economic analysis. The generalized Schaefer models provide predictions of catch, given effort, and these predictions are testable. Examples of the tracking ability of the generalized Schaefer model are given in Chapter 5 of Schrank et al. (1984).

In the next section we further describe the model and discuss

data requirements, in particular describing the measurement of fishing effort. In the third section we discuss estimation problems and the results, while in the fourth we briefly state our conclusions.

The functions of the generalized Schaefer model are fitted with data for a particular northwest Atlantic cod (*Gadus morhua*) fishery of great historical and considerable current importance; data relate to offshore fishing activity (i.e. at least several miles from land) in NAFO divisions 2J, 3K, and 3L. Cod (known as "northern cod") in this area (which encompasses the sea from the southern Labrador shelf to the northern Grand Banks) is managed by the Canadian government as a distinct stock (Government of Canada 1978). Fish management in this area has recently been the subject of international controversy between Canada and the European nations that have traditionally fished these waters, and continues to be the subject of political antagonism between two of Canada's Atlantic provinces.

## The Model and the Data

Empirical studies concerning the estimation of fisheries production functions are usually handicapped by a lack of information relating to the size of the fish resource. Direct estimation of the production function for a fishery requires biological fish population data. A circularity problem arises in that biologists often estimate the size of the fish population by assuming a given structure of the production function (e.g. Pope 1976). The results of such estimation would be appropriate if the production function utilized by the biologists were acceptable. Economists might, however, have difficulty accepting the production function most often used by biologists, the Cobb–Douglas function with both exponents constrained to be 1.

The two equations of the Schaefer model are

$$(1) \quad Q = kEP$$

and

$$(2) \quad \frac{dP}{dt} = aP - bP^2 - Q$$

where $Q$ is catch, $E$ is effort, $P$ is fish population, $t$ is time, and $k$, $a$, and $b$ are parameters to be estimated.

Since the Schaefer model is usually formulated in a continuous-time framework, empirical application of the model is encumbered by the discrete nature of the available data; an approximation procedure must be adopted before estimation can proceed. While there may be many problems involved in any scheme of approximation, an even more fundamental problem lies in Schaefer's formulation per se. Equation (1) is very restrictive in that the assumption of constant returns to each of the factors is imposed. It seems unreasonable, for instance, to expect that, given effort, catch doubles as population doubles, if only because of net and vessel capacity constraints. In any case, it was long ago settled that the magnitude of returns to scale is a testable hypothesis (Durand 1937). The extensive literature relating to the estimation of the Schaefer model (e.g. see Schaefer 1974; Walter 1975; Schnute 1977; Uhler 1980) is almost exclusively concerned with the rather limited problem of estimating only the three parameters that are unconstrained in Schaefer's formulation.

There have been a number of attempts to generalize the production function for the fishery. In one, Comitini and Huang (1967) estimated the more conventional Cobb–Douglas function:

$$(3) \quad Q = kE^{\alpha}P^{\beta}.$$

They used, as a proxy for population, the ratio of catch to effort. This is the proxy, referred to earlier, that is justified by reference to equation (1) where catch per unit effort is indeed proportional to population. Such an assumption, however, is inconsistent with the more general form of the function used by Comitini and Huang. We obtained estimates of the parameters of equation (3) by an entirely different method which requires no such proxy for population.

There are at least two examples in the literature in which fish population estimates obtained from biologists are used. In a study of the Manx herring (*Clupea harengus*) fishery, Tomkins and Butlin (1975) directly estimated equation (3) using population figures obtained from a cohort analysis. Their estimates are $\hat{\alpha} = 0.60$ and $\hat{\beta} = 0.65$, values significantly different from 1 (by a conventional two-tailed $t$-test at the 5% significance level). Similarly, in a recent study of Canadian lobster (*Homarus americanus*) fisheries, Henderson and Tugwell (1979) employed estimates of population generated by tagging experiments. Their estimates of $\hat{\alpha} = 0.48$ and $\hat{\beta} = 0.44$ for the parameters of equation (3) are also significantly different from 1. These two sets of estimates, therefore, provide support for the argument that the functional form of equation (1) is inadequate as a maintained hypothesis. As early as 1954, Gordon (1954, p. 138–140) remarked on the role that this maintained hypothesis was playing in the early literature of fisheries economics.

The generalized Schaefer model estimated here is shown in deterministic form as equations (4) and (5). We discuss details of the stochastic structure later. Equation (4), a slightly modified version of equation (3), is used to avoid problems of multicollinearity encountered during the nonlinear estimation process. Adoption of the exponential form of the constant is a mathematical convenience that changes nothing of substance in the production/population dynamics analysis. Equation (5) is a straightforward discrete version of equation (2):

$$(4) \quad Q_t = e^{k}E_t^{\alpha}P_t^{\beta}$$

$$(5) \quad P_t - P_{t-1} = aP_{t-1} - bP^2_{t-1} - W_{t-1}$$

where $Q_t$ is the total catch of cod by Newfoundland based trawlers in NAFO divisions 2J, 3K, and 3L in year $t$, $E_t$ is the total standardized effort (discussed below) expended by all Newfoundland offshore vessels fishing for northern cod in year $t$, $P_t$ is the population of northern cod at the beginning of year $t$, and $W_t$ is the total catch of northern cod by the vessels of all nations ("the world catch") in year $t$.

All population and catch figures are measured in metric tons ($t$), effort is measured in standardized days fishing, and $k$, $\alpha$, $\beta$, $a$, and $b$ are parameters to be estimated. The data are presented in Table 1.

In the NAFO divisions under consideration, offshore cod catches are taken by a variety of vessels, primarily stern and side trawlers in the 150–500 ton class and stern trawlers in the 500–1000 ton class. Lesser amounts are taken by other types of vessels as well. The primary gear used on Newfoundland vessels is the bottom otter trawl, although a variety of other gear are also used. The productivity (in terms of quantity of fish caught) of one day's fishing effort will clearly vary with vessel and gear types. Two fishermen in a dory will catch less fish in a day than will the crew of a large stern trawler, for instance. If the

TABLE 1. Data used to generate results of Tables 3 and 7 (catch in metric tons, effort in "dory-day" equivalents).

| Year | Cod catch | Bycatch | Effort | World catch | Cod catch (bycatch <30%) | Effort (bycatch <30%) |
|---|---|---|---|---|---|---|
| 1953 | 294.000 | 225.000 | 1239.968 | 113351.000 | 21.000 | 21.486 |
| 1954 | 1567.000 | 541.000 | 3947.939 | 304007.000 | 1096.000 | 2607.589 |
| 1955 | 654.000 | 465.000 | 2414.657 | 263918.000 | 269.000 | 1194.130 |
| 1956 | 366.000 | 37.000 | 682.360 | 300535.000 | 366.000 | 682.360 |
| 1957 | — | — | — | 275733.000 | — | — |
| 1958 | 69.000 | 18.000 | 129.682 | 217089.000 | 69.000 | 129.682 |
| 1959 | 1021.000 | 371.000 | 2609.617 | 329572.000 | 869.000 | 1951.627 |
| 1960 | 1124.000 | 375.000 | 2753.809 | 393577.000 | 1124.000 | 2753.809 |
| 1961 | 1123.000 | 237.000 | 2022.709 | 498078.000 | 1111.000 | 1998.340 |
| 1962 | 402.000 | 117.000 | 1242.870 | 502752.000 | 374.000 | 1096.650 |
| 1963 | 463.000 | 197.000 | 1389.090 | 490884.000 | 124.000 | 389.920 |
| 1964 | 3563.000 | 1590.000 | 9650.516 | 561753.000 | 897.000 | 2631.959 |
| 1965 | 1721.000 | 924.000 | 5250.645 | 510785.000 | 201.000 | 724.468 |
| 1966 | 3662.000 | 1658.000 | 10181.754 | 514926.000 | 815.000 | 2158.018 |
| 1967 | 5828.000 | 2059.000 | 19461.887 | 600200.000 | 4486.000 | 14751.598 |
| 1968 | 10037.000 | 3017.000 | 34037.402 | 783204.000 | 7307.000 | 23176.645 |
| 1969 | 6458.000 | 3097.000 | 25774.070 | 689466.000 | 2484.000 | 8297.898 |
| 1970 | 6226.000 | 2851.000 | 21600.211 | 486441.000 | 1289.000 | 3218.545 |
| 1971 | 4351.000 | 2989.000 | 21799.871 | 420517.000 | 197.000 | 827.350 |
| 1972 | 627.000 | 340.000 | 4038.983 | 454590.000 | 259.000 | 1285.260 |
| 1973 | 609.000 | 294.000 | 3405.936 | 354509.000 | 281.000 | 1720.902 |
| 1974 | 200.000 | 54.000 | 1206.864 | 372647.000 | 128.000 | 622.430 |
| 1975 | 211.000 | 141.000 | 1213.667 | 287508.000 | 77.000 | 400.694 |
| 1976 | 1240.000 | 498.000 | 6691.152 | 214220.000 | 786.000 | 4203.141 |
| 1977 | 2687.000 | 1442.000 | 14542.832 | 172720.000 | 1413.000 | 6771.773 |
| 1978 | 12754.000 | 3759.000 | 36417.148 | 138559.000 | 9814.000 | 25011.418 |
| 1979 | 36462.000 | 7277.000 | 82353.250 | — | 32147.000 | 65957.312 |

NOTE: Cod catch is the Newfoundland offshore "main species" catch. Small quantities of cod caught as bycatch to other fisheries operations are ignored. World catch is the total cod catch in divisions 2J, 3K, and 3L. Bycatch is the catch of non-cod species associated with Newfoundland offshore cod harvesting operations.

production function is to relate to the entire fishery, and not to a single gear–vessel combination, then a homogeneous effort variable that is meaningful in the context of data generated by each of the alternative fishing techniques must be used. The method we adopt is to establish relative productivity weights for all gear–vessel combinations used in the Newfoundland groundfishery. We use a multiple regression analysis to obtain these weights, the details of the technique being presented in Schrank et al. (1980). Our technique is similar to that introduced by Robson (1966) and subsequently used by Carlson (1975) and Sissenwine and Bowman (1978). These authors, however, had the advantage of access to specific data concerning individual vessels. Hannesson (1983), referred to above, used a weaker technique that is, in general, both intransitive and noninvertible (see Appendix 2 of Schrank et al. 1980 for a discussion of the desirable properties of relative productivity estimates).

The weights permit us to evaluate one day's fishing effort for any gear type in terms of a specific gear–vessel combination taken as datum. The regression analysis is based on a pooled sample of time series and cross-section monthly data for the Newfoundland groundfishery for the period 1953–79. As datum, we arbitrarily choose the least efficient gear–vessel combination used in the Newfoundland codfishery, handlining from small motorboats, or "dories."

The effort variable used in the estimation of the production function is denominated in "dory units" or "equivalent days fishing by handlining from a dory." This variable is computed as a weighted sum of the days fishing reported for each gear–vessel combination used in the offshore northern cod fleet, the weights being the productivity of that particular gear–vessel combination relative to the productivity of dory handlining (see Table 2).

## Results

The model (equations (4) and (5)) contain five unknown parameters to be estimated: $k$, $\alpha$, $\beta$, $a$, and $b$; two readily measured variables: $Q_t$ and $W_t$; the variable $E_t$ as defined in the last section; and the unmeasurable variable $P_t$. Since the population variable appears in both equations, by suitable substitution we can obtain a single equation consisting of only unknown parameters and measurable variables.

Lagging equation (4) one period generates an expression for $P_{t-1}$ that can be substituted into equation (5). This expression then generates another for current population that can be substituted into equation (4) to yield the estimation equation (where the expression in square brackets will be denoted below as $P_t^*$):

$$(6)\quad Q_t = e^k E_t^{\alpha}\left[(1+a)\left(\frac{Q_{t-1}}{e^k E_{t-1}^{\alpha}}\right)^{1/\beta} - b\left(\frac{Q_{t-1}}{e^k E_{t-1}^{\alpha}}\right)^{2/\beta} - W_{t-1}\right]^{\beta}.$$

Annual time series on $Q_t$, $E_t$, and $W_t$ for the period 1954–78 were used with the modified Gauss–Newton (BMDP3R) nonlinear estimation routine incorporated into the Biomedical Computer Programs package of the University of California at Los Angeles (Dixon and Brown 1979).

TABLE 2. Relative productivity weights for various gear-vessel combinations used in the Newfoundland offshore groundfishery.

| Vessel type | Gear type | Relative productivity weight |
|---|---|---|
| Large longliners (50–149.9 tons) | Gill nets | 7.974 |
| | Longlines | 12.584 |
| | Cod traps | 11.111 |
| | Bottom otter trawls (side trawls) | 10.734 |
| | Bottom otter trawls (stern trawls) | 12.708 |
| Trawlers (150–499.9 tons) | Longlines | 12.743 |
| | Bottom otter trawls (side trawls) | 24.370 |
| | Bottom otter trawls (stern trawls) | 27.640 |
| | Midwater otter trawls (side trawls) | 33.796 |
| | Midwater otter trawls (stern trawls) | 34.067 |
| Trawlers (≥500 tons) | Bottom otter trawls (side trawls) | 23.206 |
| | Bottom otter trawls (stern trawls) | 33.094 |
| | Midwater otter trawls (stern trawls) | 60.718 |

Problems of estimating a highly nonlinear functon of five unknown parameters are formidable: there may be many local optima, making estimation of the global solution more difficult; for certain combinations of parameter and variable values the function may be undefined; and for other combinations of parameter and variable values the computational procedures may simply not converge. We use fairly stringent convergence criteria throughout. For convergence to have occurred, from one iteration to the next there must be no change to four significant digits in all parameter estimates and to five significant digits in the residual sum of squares.

Since the success of the iterative procedure in achieving convergence depends on the choice of the set of initial conditions assumed for the parameters, we use an elaborate process to determine suitable initial values.

The process starts with a grid search procedure in which the parameter values of $\alpha$ and $\beta$ are permitted to vary from 0.4 to 1.5, the probable range of these parameters. Given an assumed pair of values for $\alpha$ and $\beta$, we obtain estimates of $a$, $b$, and $k$ by linear estimation. Having started with an assumed pair of values for $\alpha$ and $\beta$, and having then determined values for the remaining parameters, we use these five values as a set of initial conditions for the nonlinear estimation process. The entire process is replicated for numerous combinations of $\alpha$ and $\beta$ within the allowable range. In most cases, for a set of initial conditions, the nonlinear estimation process fails to converge. For those sets of initial conditions for which the nonlinear estimation process does converge, we have found that they converge to the same set of solutions. We therefore believe that, within the allowable range of $\alpha$ and $\beta$, we have located the global minimum.

Taking the logarithm of equation (6), we can obtain the derivatives required as input into the BMDP3R program:

$$(7)\quad \frac{\partial \ln Q_t}{\partial k} = 1 - \left[(1+a)\frac{P_{t-1}}{P_t^*} - 2b\frac{P^2_{t-1}}{P_t^*}\right]$$

$$(8)\quad \frac{\partial \ln Q_t}{\partial \alpha} = \ln E_t - \left[(1+a)\frac{P_{t-1}}{P_t^*} - 2b\frac{P^2_{t-1}}{P_t^*}\right]\ln E_{t-1}$$

$$(9)\quad \frac{\partial \ln Q_t}{\partial \beta} = \ln P_t^* - \left[(1+a)\frac{P_{t-1}}{P_t^*} - 2b\frac{P^2_{t-1}}{P_t^*}\right]\ln P_{t-1}$$

$$(10)\quad \frac{\partial \ln Q_t}{\partial a} = \beta\frac{P_{t-1}}{P_t^*}$$

$$(11)\quad \frac{\partial \ln Q_t}{\partial b} = -\beta\frac{P^2_{t-1}}{P_t^*}.$$

Comparison of equation (7) with equations (10) and (11) shows that $\partial \ln Q_t/\partial k$ is perfectly collinear with $\partial \ln Q_t/\partial a$ and $\partial \ln Q_t/\partial b$. With equation (3) as the production function, collinearity would be imperfect but serious. By adopting equation (4) instead, as we have done, perfect collinearity occurs, and the following solution to the multicollinearity problem is apparent. The method of BMDP3R involves obtaining the Taylor expansion of the logarithm of equation (6) about the trial values of the parameters and shifting the known components of this expansion to the left side of the equation to form a composite regressand. The right side is then

$$(12)\quad k\frac{\partial \ln Q_t}{\partial k} + \alpha\frac{\partial \ln Q_t}{\partial \alpha} + \beta\frac{\partial \ln Q_t}{\partial \beta} + a\frac{\partial \ln Q_t}{\partial a} + b\frac{\partial \ln Q_t}{\partial b}$$

where all partial derivatives are evaluated at the trial values of the parameters and where the first, fourth, and fifth terms in this expression are perfectly collinear. By substituting equations (10) and (11) into equation (7) and defining

$$(13)\quad a' = a - \frac{(1+a)k}{\beta}$$

and

$$(14)\quad b' = b - \frac{2bk}{\beta}$$

expression (12) becomes

$$(15)\quad k + \alpha\frac{\partial \ln Q_t}{\partial \alpha} + \beta\frac{\partial \ln Q_t}{\partial \beta} + a'\frac{\partial \ln Q_t}{\partial a} + b'\frac{\partial \ln Q_t}{\partial b}.$$

The problem of perfect multicollinearity is solved, parameters $k$, $\alpha$, $\beta$, $a'$, and $b'$ can be estimated, and estimates of $a$ and $b$, the parameters of the population dynamics equation, can be obtained by inverting equations (13) and (14). The results are shown in Table 3.

We also attempted to estimate a more general, asymmetric population dynamics equation but this experiment was unsuccessful. The generalization involved changing the term $P^2$ in equation (2) to $P^n$, where $n$ is a parameter to be estimated. This change has the effect of changing the exponent $2/\beta$ in equation (6) to $n/\beta$. With six parameters being estimated, an expression for $\partial \ln Q_t/\partial n$ would be added to the set of equations (7)–(11). This derivative expression proved to be highly (but not perfectly) collinear with the derivative of equation (11). No solution to this collinearity problem was apparent without seriously altering the specification of the model. Because of this problem, and considering Pella and Tomlinson's (1969, p. 442–443) conclusion that, even when the population dynamics equation is skewed, key parameter and decision variable estimates are virtually unchanged from the values they take in the symmetric case, we decided to abandon the effort to generalize the population dynamics equation.

When a model exhibits favorable statistical properties, the estimates obtained from nonlinear estimation routines such as that in BMDP3R are approximately normal. It is clear from Table 3 that, under the assumption of favorable properties, each of the five parameter estimates is significantly different from zero under the conventional 5% two-tailed significance test. This result suggests that the problems of partial multicollinearity have been overcome. There are additional problems, however, and the test results must be viewed cautiously. Equations (4) and (5) are both stochastic and the addition of a multiplicative error to equation (4) and an additive error to equation (5) results in the estimation equation (6) containing multiplicative (as well as additive) errors in variables. Hannesson (1983, p. 974) justified using the multiplicative stochastic term in equation (4); the additive term in equation (5) is conventional. It is clear from Chow's (1983, Chap. 7) discussion of nonlinear estimation that, under these conditions, the desirable properties of nonlinear estimation procedures fail. As Uhler (1980) has shown, each of the various linear methods proposed for estimating the restricted conventional Schaefer model suffers from errors in variables bias. The generalized nonlinear model presented here is no different in this regard, except that even less is known about the properties of estimators when there are multiplicative errors in variables (as in our case) than when there are simply additive errors in variables (as in the conventional Schaefer case).

While he showed that the bias in the estimates might be serious, Uhler closed his paper with evidence that the implications of the bias in specific applications depend critically upon the details of the situation being analyzed, and in certain cases might be relatively minor. It seems reasonable, therefore, to continue applying Schaefer-type models despite the statistical problems. It also seems reasonable, however, that the search for a solution to the errors in variables problem in the context of fisheries production models should continue in the realm of the generalized Schaefer model. This is because the restricted conventional Schaefer formulation adds a potentially serious specification error to the other problems encountered in estimation.

TABLE 3. Results of nonlinear estimation using annual data for 1954–79 (excluding 1957).

| Parameter | Estimate | Asymptotic SD |
|---|---|---|
| $k$ | −12.012 | 3.380 |
| $\alpha$ | 0.975 | 0.045 |
| $\beta$ | 0.794 | 0.223 |
| $a'$ | 34.525 | 9.147 |
| $b'$ | $0.200 \times 10^{-4}$ | $0.053 \times 10^{-4}$ |

TABLE 4. Properties of estimates reported in Table 3.

| Property | Value |
|---|---|
| $R^2$ | 0.976 |
| $a$ | 1.203 |
| $b$ | $0.640 \times 10^{-6}$ |
| Maximum population = $a/b$ | 1 879 304 |
| Maximum sustainable yield population = $a/2b$ | 939 652 |
| Maximum sustainable yield $= \frac{a}{2b} \cdot \frac{a}{2}$ | 565 006 |

Our maximum sustainable yield estimate for northern cod (Table 4) is virtually equivalent to the 550 000 t figure given by Pinhorn (1976, p. 6). In Table 5, we compare the population estimates from the generalized Schaefer analysis with a time series of biomass estimates obtained by Wells and Bishop (1980) using cohort analysis. The two sets of figures, while of the same order of magnitude, are widely divergent with substantially greater variability in the Wells–Bishop results. Our procedure generates population estimates that minimize the sum of squared errors in estimating catch. Cohort analysis provides estimates of population from an entirely different statistical basis. There is really very little information available to render a judgment on whether one population series better accounts for reality than the other. To obtain comparable parameter estimates, however, we used the Wells–Bishop figures to directly estimate equation (4) using ordinary least squares. The estimate of $\beta$ using the Wells–Bishop data is substantially different from the results of nonlinear estimation (see Table 6), but no a priori information is available to permit us to express a preference between the two sets of results.

No mention has yet been made of the role of bycatches, a topic of considerable current interest in fisheries analysis (e.g. see Huppert 1979). Offshore vessels, when catching northern cod, also catch substantial quantities of flounder and sole. The results of an informal survey of trawler operators were inconclusive as to how bycatches affect fishing decisions; the results

TABLE 5. Population estimates of cod in ICNAF divisions 2J, 3K, and 3L (in thousands of metric tons).

| Year | Population estimate[a] | Biomass estimate[b] |
|---|---|---|
| 1954 | 1184.6 | — |
| 1955 | 1559.1 | — |
| 1956 | 1211.5 | — |
| 1957 | — | — |
| 1958 | 1540.7 | — |
| 1959 | 1644.8 | — |
| 1960 | 1519.2 | — |
| 1961 | 1479.2 | — |
| 1962 | 1226.6 | 2875.0 |
| 1963 | 1158.5 | 2635.0 |
| 1964 | 1205.3 | 2472.0 |
| 1965 | 1269.3 | 2305.0 |
| 1966 | 1201.6 | 2250.0 |
| 1967 | 1297.4 | 2406.0 |
| 1968 | 1050.0 | 2306.0 |
| 1969 | 865.0 | 2034.0 |
| 1970 | 762.0 | 1699.0 |
| 1971 | 1123.9 | 1673.0 |
| 1972 | 759.1 | 1593.0 |
| 1973 | 421.7 | 1304.0 |
| 1974 | 656.8 | 1017.0 |
| 1975 | 537.7 | 672.0 |
| 1976 | 669.9 | 556.0 |
| 1977 | 852.0 | 874.0 |
| 1978 | 910.6 | 1185.0 |
| 1979 | 1677.2 | 1573.0 |

[a]Computed from the results reported in Table 3.
[b]Source: Wells and Bishop (1980, p. 12).

TABLE 6. Comparative regression results using nonlinear least squares (from Table 3) and using OLS with Wells–Bishop data (SE in parentheses).

| Parameter | Estimate (nonlinear) | Estimate (OLS) |
|---|---|---|
| $\alpha$ | 0.975 | 1.088 |
| | (0.045) | (0.044) |
| $\beta$ | 0.794 | 0.421 |
| | (0.223) | (0.121) |
| $R^2$ | 0.976 | 0.977 |

of the survey indicated that behaviour ranged from operators instructing skippers to seek various bycatches depending upon quotas, to skippers choosing fishing locations depending upon informal total catch optimization, and to simply taking the bycatch as it comes and treating income from the bycatch essentially as the returns from the sale of a free good. Rarely is the bycatch less than 20% of the total catch in northern cod operations; it is often one third of the total catch and occasionally nearly one half.

We experimented with a number of analytical methods of handling bycatches but found that they either required heroic assumptions that we were unwilling to make or they substantially complicated an already difficult estimation problem. To test the hypothesis that we could simply neglect the bycatch, we applied our estimation procedure to data consisting of observations in which there was a relatively small bycatch, no more than 30% of the total catch being a species other than cod. The results (Tables 7 and 8) are almost identical to those obtained when the existence of a bycatch was ignored (Tables 3 and 4). We therefore accept the hypothesis that we can neglect the bycatch.

TABLE 7. Results of nonlinear estimation (bycatch less than 30% of total catch).[a]

| Parameter | Estimate | Asymptotic SD |
|---|---|---|
| $k$ | $-11.841$ | 4.686 |
| $\alpha$ | 0.976 | 0.051 |
| $\beta$ | 0.782 | 0.309 |
| $a'$ | 34.824 | 12.932 |
| $b'$ | $0.205 \times 10^{-4}$ | $0.075 \times 10^{-4}$ |

[a]Annual data for 1955–79 excluding 1957 (for which data are unavailable) were used. There was only one observation for 1954 so this year was omitted. In 1955, there was only a negligible cod catch where the bycatch was less than 30% but there was a substantial cod catch with a bycatch of 30–33%. For this observation only, therefore, we raised the bycatch limit to 33%.

TABLE 8. Properties of estimates reported in Table 7 (bycatch less than 30% of total catch).

| Property | Value |
|---|---|
| $R^2$ | 0.968 |
| $a$ | 1.220 |
| $b$ | $0.657 \times 10^{-6}$ |
| Maximum population $= a/b$ | 1 857 978 |
| Maximum sustainable yield population $= a/2b$ | 928 989 |
| Maximum sustainable yield $= \frac{a}{2b} \cdot \frac{a}{2}$ | 566 728 |

## Conclusion

We have estimated the exponents of the Cobb–Douglas production function for a fishery using a logistic population dynamics equation. While the Schaefer model has been a standard in its field for nearly 30 yr, the direct estimation of these parameters in the absence of fish population estimates has not previously succeeded.

There are nearly constant returns to effort, with the estimated value of the appropriate exponent equal to 0.975. Returns to population are somewhat lower, however, with a value of 0.794. Neither of these estimates is significantly different from 1, and our results therefore do not lead to the rejection of the Schaefer model, for the northern cod stock at least. Of course, this result need not be true of other fish populations, such as those used in the Tomkins and Butlin (1975) and Henderson and Tugwell (1979) studies.

Despite the result that our estimate of returns to population is not significantly different from 1, the fact that our estimate of the appropriate parameter is numerically well below 1 may have serious policy implications. We have, for example, performed simulations that show that, even for very conservative assumptions, equilibrium catch and population figures can be substantially different depending upon whether our estimates or the original Schaefer assumptions are used. As a result, steady-state quota allocations and total allowable catch paths to the steady state may be strongly affected by the production assumptions made.

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## References

ANDERSON, L. G. 1977. The economics of fisheries management. Johns Hopkins University Press, Baltimore, MD. 214 p.

CARLSON, E.W. 1975. The measurement of relative fishing power using cross section production functions. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 168: 84–98.

CHOW, G. C. 1983. Econometrics. McGraw-Hill Book Company, New York, NY. 432 p.

CLARK, C. W. 1976. Mathematical bioeconomics. John Wiley & Sons, New York, NY. 352 p.

COMITINI, S., AND D. S. HUANG. 1967. A study of production and factor shares in the halibut fishing industry. J. Polit. Econ. 75: 366–372.

DIXON, W. J., AND M. B. BROWN. 1979. BMDP-79: biomedical computer programs P. series. University of California Press, Berkeley, CA. 880 p.

DURAND, D. 1937. Some thoughts on marginal productivity with special reference to Professor Douglas' analysis. J. Polit. Econ. 45: 740–758.

GOH, B. S. 1980. Management and analysis of biological populations. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands. 288 p.

GORDON, H. S. 1954. Economic theory of a common-property resource. J. Polit. Econ. 62: 124–142.

GOVERNMENT OF CANADA. 1978. Resource prospects for Canada's Atlantic fisheries: 1979–85. Department of Fisheries and Oceans, Ottawa, Ont. 60 p.

HANNESSON, R. 1983. Bioeconomic production function in fisheries: theoretical and empirical analysis. Can. J. Fish. Aquat. Sci. 40: 968–982.

HENDERSON, J. V., AND M. TUGWELL. 1979. Exploitation of the lobster fishery: some empirical results. J. Environ. Econ. Manage. 6: 287–296.

HUPPERT, D. D. 1979. Implications of multipurpose fleets and mixed stocks for control policies. J. Fish. Res. Board Can. 36: 845–853.

KIM, C. 1983. Optimal management of multi-species North Sea fishery resources. Weltwirtschaftliches Arch. 119: 138–151.

PELLA, J. J., AND S. J. TOMLINSON. 1969. A generalized stock production model. Bull. Inter-Am. Trop. Tuna Comm. 13: 421–496.

PINHORN, A. T. 1976. Living marine resources of Newfoundland and Labrador: status and potential. Bull. Fish. Res. Board Can. 194: 64 p.

POPE, J. G. 1976. The application of mixed fisheries theory to the cod and redfish stocks of Subarea 2 and Division 3K. ICNAF Select. Pap. 1: 163–169.

ROBSON, D. S. 1966. Estimation of the relative fishing power of individual ships. ICNAF Res. Bull. 3: 5–14.

SCHAEFER, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull. Inter-Am. Trop. Tuna Comm. 1: 27–56.

1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Bull. Inter-Am. Trop. Tuna Comm. 2: 247–285.

1974. Methods of estimating effects of fishing on fish population. Trans. Am. Fish. Soc. 103: 231–241.

SCHNUTE, J. 1977. Improved estimates from the Schaefer production model: theoretical considerations. J. Fish. Res. Board Can. 34: 583–603.

SCHRANK, W. E., N. ROY, AND E. TSOA. 1980. The relative productivity and cost-effectiveness of various fishing techniques in the Newfoundland groundfishery. Discussion Paper No. 180. Economic Council of Canada, Ottawa, Ont. 304 p.

SCHRANK, W. E., E. TSOA, AND N. ROY. 1984. An econometric model of the Newfoundland groundfishery: estimation and simulation. A report submitted to the Department of Fisheries and Oceans. Department of Economics, Memorial University of Newfoundland, St. John's, Nfld. 356 p.

SISSENWINE, M. P., AND E. W. BOWMAN. 1978. An analysis of some factors affecting the catchability of fish by bottom trawls. ICNAF Res. Bull. 13: 81–87.

STOCKER, M., AND R. HILBORN. 1981. Short-term forecasting in marine fish stocks. Can. J. Fish. Aquat. Sci. 38: 1247–1254.

TOMKINS, J. M., AND J. A. BUTLIN. 1975. Theoretical and empirical approach to fisheries economics. Am. J. Agric. Econ. 26: 105–125.

UHLER, R. S. 1980. Least squares regression estimates of the Schaefer production model: some Monte Carlo simulation results. Can. J. Fish. Aquat. Sci. 37: 1284–1294.

WALTER, G. G. 1975. Graphical methods for estimating parameters in simple models of fisheries. J. Fish. Res. Board Can. 32: 2153–2168.

WELLS, R., AND C. A. BISHOP. 1980. Some recent changes in cod stock in Divisions 2J and 3KL. Res. Doc. 8/VI/101, No. N156, NAFO, Dartmouth, N.S. 15 p.

# Determinants of Catching Power in the British Columbia Salmon Purse Seine Fleet

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Hilborn, R., and M. Ledbetter. 1985. Determinants of catching power in the British Columbia salmon purse seine fleet. Can. J. Fish. Aquat. Sci. 42: 51–56.

We show that vessel attributes such as age, length, tonnage, and horsepower will account for less than 10% of the differences in catch between vessels in the British Columbia salmon purse seine fleet. The vessel effect is defined as repeatable differences in catch between vessels. This effect accounts for 30–34% of the differences, and we infer that the unmeasured skipper, crew, and net effects are responsible for 20–24% of the variance in catch. Vessels are specialized by area, with many boats performing well in one area and poorly in another. When fishing area is added as a treatment, area specialization accounts for roughly half of the vessel effect. In fisheries where local knowledge and experience are important, attempts to calibrate catch per unit effort data based on vessel attributes may not work well if skipper skills are a major determinant of catch. Additionally, skipper skill will greatly impede attempts to reduce catching power by elimination of vessels through buy back proposals, since vessels, and not skippers, will be eliminated.

Nous avons constaté que certaines caractéristiques comme l'âge, la longueur, le tonnage du bateau, la puissance du moteur expliquent moins de 10 % de différences observées entre les prises des différents bateaux à senne coulissante de la flotte de pêche au saumon de la Colombie-Britannique. L'influence du bateau se définit comme des différences de prises reproductibles d'un bateau à l'autre. Cette influence justifie de 30 à 34 % des différences observées ; nous en déduisons que le capitaine, l'équipage et le filet justifient de 20 à 24 % des variations. Il y a des zones de spécialisation : pour bon nombre de bateaux, les prises sont bonnes dans une zone et mauvaise dans l'autre. Si l'on tient compte de la zone de pêche, la spécialisation justifie à peu près la moitié de l'influence du bateau. Dans les pêches où la connaissance des lieux et l'expérience comptent beaucoup, il peut être difficile de mesurer la prise par effort de pêche si les aptitudes du capitaine ont un effet déterminant sur l'importance de la prise. En outre, les efforts déployés pour réduire les capacités de prise en rachetant des bateaux peuvent être considérablement compromis, car, par ce moyen, on retire des bateaux de l'opération, non des capitaines.

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Many of the world's major fisheries use catch per unit of effort as an index of stock abundance. Since technology rarely stands still for the convenience of managers, agencies such as the International Pacific Halibut Commission and the Inter-American Tropical Tuna Commission are involved in repeated statistical research on determining the relative catching power of different types of vessels to produce a "standardized" unit of effort which serves as the basis of catch per unit effort indices of abundance. In an ICES symposium (Pope 1975) devoted to studies relating the catch of individual vessels to their measurable attributes such as length, tonnage, etc., it was found that despite the obvious difference in catching power between old small boats and larger new ones, particularly in fisheries where distance travelled or volume swept by a net is an obvious factor in catching power, the attempts to relate catch to physical attributes often produces relatively small correlations between catch and attributes. A significant exception appears to be in the Icelandic cod (*Gadus morhua*) fishery where Pálsson and Durrenberger (1982) showed that vessel size and number of trips accounted for most of the variation in catch.

Two explanations of poor correlation are possible: either fishing is a highly stochastic process in which luck is a major factor, or some unmeasured attribute of the harvesting unit is important in determining catching power. Commercial fishermen have suggested that local knowledge of vessel operators (skippers) is a key factor in the British Columbia salmon purse seine fishery. If skipper knowledge is an important factor in determining catching power, it should be exhibited in this fishery where local geography, tides, and timings of runs are important and many individual locations are fished. Most seine boats operate in several areas in a given season, so contrast in skipper's skill is available on a short time period. In this paper we explore the relationships between catching power, measured vessel attributes, the vessel effect, and geographic location to assess the relative importance of these factors in determining catch.

## Source of Data

All commercial fishing vessels in British Columbia are registered annually with the Department of Fisheries and Oceans (DFO), and provide information such as length, net and gross tonnage, horsepower, year built, assessed value, etc. We

will refer to these data as vessel attribute data. Salmon seine fisheries are normally open for 1–3 d, beginning at 18:00 Sunday. At the end of the fishery, or possibly every day, the seine boats deliver their catch to a company packer. At the time of delivery, a sales slip is filled out giving vessel number, weight and number of species caught, value of fish, and the area fished. These data are referred to as the sales slip data. The attribute and sales slip data were made available to us by DFO for the five years 1973–77. For purposes of confidentiality, the vessel registration numbers were coded so that we could not identify the actual vessel.

We compressed the sales slip data from catch by day, species, and statistical area (See Hilborn and Ledbetter 1979 for details) to value of catch by week and aggregate area. Here we discuss catches in two of our aggregate areas only (see map 1, Hilborn and Ledbetter 1979), Johnstone Strait (statistical areas 12 and 13) and Juan de Fuca (statistical area 20).

## Description of British Columbia Purse Seine Operations

British Columbia purse seiners fish for salmon over much of the British Columbia coast, but the two major fisheries, and the ones we analyze in this paper, take place in the Johnstone Strait between the Mainland and Vancouver Island and in Juan de Fuca Strait off the southwest tip of Vancouver Island. These two fisheries contrast the possible conditions in British Columbia salmon seine operations. Johnstone Strait is characterized by strong tides, local reefs, and protected waters. The Juan de Fuca fishery is characterized by open water, high seas, and much less geographic variation. The Johnstone Strait fishery is the dominant seine fishery in British Columbia; vessels target primarily on Fraser River sockeye (*Oncorhynchus nerka*), pink (*Oncorhynchus gorbuscha*), and chum salmon (*Oncorhynchus keta*). Well over 300 boats may operate in this area during periods of peak abundance. The lower half of the strait (statistical area 13) is a very narrow channel with strong tidal currents. The major fishing strategy is called the pointset: the seine net is attached to a point of land and towed in a cup shape, being held against the current by the attachment to land at one end and by the seine boat at the other. After being held in this position for 10–30 min, the net is closed and hauled on board using a power drum. In exceptional events when thousands of fish have been captured, the seine must be emptied by brailling the net before being hauled on board. The other type of fishery that takes place in Johnstone Strait is called an open set: an unpowered skiff on a sea anchor is substituted for the stationary tie up. In general, point sets are preferred until line-ups at desirable points become too long. As waiting times increase, many skippers begin to make open sets in less congested areas. The major exception to this strategy takes place at the north end of Johnstone Strait off Malcolm Island where the normal mode of fishing is the open set.

The Juan de Fuca fishery is quite different in that it occurs on the exposed outer coast of British Columbia at an imaginary line between a geographic point in British Columbia and one in Washington State. The fishery consists of vessels making open sets just inside the line. Line-ups form on the boundary. In a good week, there might be 100 boats sharing 10 line-up spots, each boat waiting for its turn to set the net every 5 h or so.

## Determinants of Catching Power

We explore the role of vessel attributes and skipper skill in determining harvest levels by comparing the Johnstone Strait and Juan de Fuca fisheries. If vessel attributes are important and are independent, we expect vessels to do well in both areas. This is certainly the popular conception; we hear concerns about the development of a new, highly efficient, mobile purse seine fleet with greatly increased catching power. We have never heard a public description of a fleet that is geographically specialized, although fishermen will mention it as soon as different areas are discussed. Therefore, the alternative is to believe that vessels, or skippers, are specialized, and those doing well in one area are less skillful in other areas. This specialization might be difficult to detect if few boats fish both areas, but fortunately many vessels move between these areas and we can determine relative performances in each fishery.

## Measurement of Performance

Ideally, we could construct an analysis of variance (ANOVA) model in which vessel, area, week effects, and interactions could be separated. The form of his ANOVA would be

$$(1)\quad C = \bar{C} + V + A + W + VA + VW + AW$$

where $C$ is the catch of a particular vessel in an area and a week, $\bar{C}$ is the average catch, $V$ is the vessel effect, $A$ is the area effect, $W$ is the week effect, and $VA$, $VW$, and $AW$ are interaction effects. An analysis of the complete, coastal data set would include appoximately 600 vessels fishing 15 wk per year in variable combinations of eight aggregate areas. This ANOVA would be very large (beyond the available University of British Columbia software) and would be highly nonorthogonal, since vessels generally fish in one area each week. In addition, we are not particularly interested in area differences or weekly differences; we know they are different (see Hilborn and Ledbetter 1979).

As an initial step, we compute a vessel's annual performance measure by area as

$$(2)\quad P_{ij} = \frac{1}{n}\sum_{k=1}^{n}(C_{ijk} - \bar{C}_{jk})$$

where $P_{ij}$ is the performance of the $i$th vessel in the $j$th area, $n$ is the number of weeks a vessel fished in area $j$, $C_{ijk}$ is the value of fish caught by vessel $i$ in area $j$ in week $k$, and $\bar{C}_{jk}$ is the average value of fish caught per vessel in area $j$ and week $k$. This performance measure corrects for weekly differences in salmon abundance and for the number of weeks fished by a vessel. The performance index is used in the following analyses.

The performances of vessels fishing Juan de Fuca and Johnstone Strait are graphically illustrated relative to both fisheries in Fig. 1. Note that some vessels did well in both areas, some poorly in both, and some well in one area and poor in another. The number of vessels in each of these four classes for each year from 1973 to 1977 is given in Table 1. There is remarkable year-to-year constancy in these data.

## Vessel Attributes

Fishermen suggest that the major vessel attribute likely to affect performance is length of vessel; small boats do not

TABLE 1. Number of seine vessels with above or below average performance in the Juan de Fuca and Johnstone Strait fisheries, 1973–77 (JS = Johnstone Strait; JdeF = Juan de Fuca).

| Year | Below average both areas | Below average JS, above average JdeF | Above average JS, below average JdeF | Above both areas |
|---|---|---|---|---|
| 1973 | 53 | 25 | 27 | 20 |
| 1974 | 53 | 30 | 28 | 17 |
| 1975 | 54 | 38 | 15 | 22 |
| 1976 | 51 | 26 | 28 | 20 |
| 1977 | 53 | 34 | 23 | 23 |

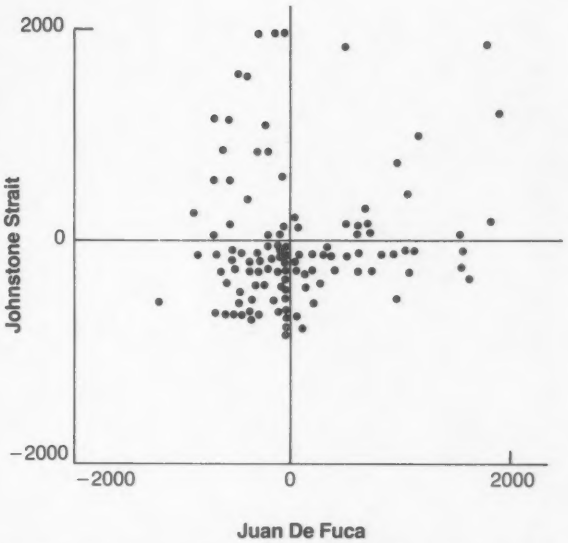


FIG. 1. Vessel performance in the Juan de Fuca fishery plotted against vessel performance in the Johnstone Strait fishery (1973). Performance in landed value above or below the mean in that area, measured in dollars per week.

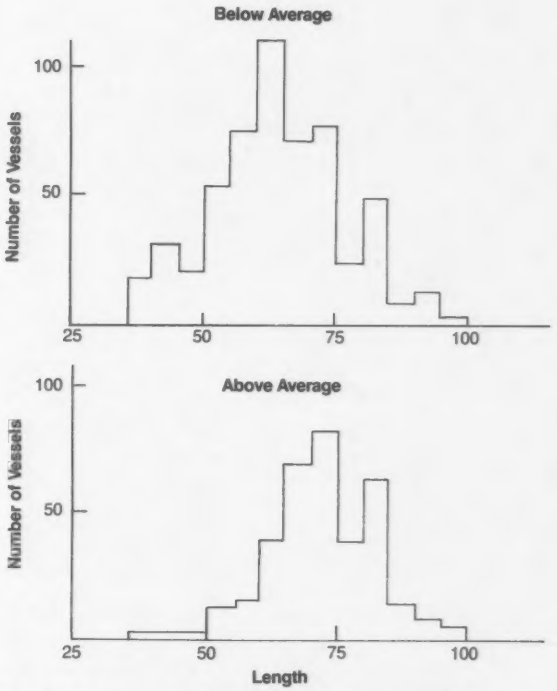


FIG. 2. Frequency distribution of length of vessels performing above and below average in 1973–77 in the Juan de Fuca fishery.

perform well in the Juan de Fuca fishery because of higher seas and larger nets. Indeed, fishermen often make a distinction between outside boats and the smaller inside boats. The distribution of lengths of vessels for boats doing above average and below average in Juan de Fuca in 1973 is shown in Fig. 2. The only obvious difference is that very few small boats were above average in Juan de Fuca. The average length of boats in each class defined by the four quadrants of Fig. 1 for 1973–77 is given in Table 2. The category frequencies are constant among years.

Instead of looking at individual vessel sizes, we can perform a regression of vessel performance on year built, listed value, horsepower, gross tonnage, and length; this analysis should account for most of the pertinent physical attributes of the vessel. The results of this regression and the ANOVA tables are given in Table 3. Note that the amount of variation explained is very small, $r^2 = 0.04$ for Johnstone Strait and $r^2 = 0.12$ for Juan de Fuca. The higher correlation in Juan de Fuca is little consolation to one who believes that vessel attributes are important.

The regression correlation coefficients are, of course, highly significant, since we have large sample sizes, but we must look

TABLE 2. Average length of vessels by the four performance categories for Johnstone Strait (JS) and Juan de Fuca (JdeF).

| | Average length (m) | | | |
|---|---|---|---|---|
| Year | Bad both | Bad JdeF, good JS | Good JdeF, bad JS | Good both |
| 1973 | 17.7 | 19.2 | 21.3 | 20.7 |
| 1974 | 18.3 | 18.9 | 20.4 | 20.7 |
| 1975 | 18.3 | 19.5 | 20.7 | 19.8 |
| 1976 | 18.9 | 19.2 | 21.3 | 19.5 |
| 1977 | 17.7 | 18.9 | 20.4 | 20.1 |

elsewhere for the cause of differences in catches between vessels. The two causal agents (which are not represented as independent measurements in our data set) are random chance and a combination of factors: skipper skill, crew skill, and the design of the net. These three physical factors are closely

TABLE 3. Regression of individual vessel performance on vessel attributes. Only vessels fishing all five years (1973–77) included.

Johnstone Strait

| Variable | Coefficient | *t*-statistic | Probability |
|---|---|---|---|
| Constant | −852.96 | −6.0477 | 0.0000 |
| Year built | 2.9046 | 2.7320 | 0.0064 |
| Estimate value | $-0.19436 \times 10^{-2}$ | −0.88494 | 0.9295 |
| Horsepower | 0.17792 | 0.71079 | 0.4773 |
| Length | 0.13270 | 4.5552 | 0.0000 |
| Gross tonnage | −1.6456 | −1.3727 | 0.1700 |

| Source | df | Sum of squares | Mean square | *F*-statistic | Probability |
|---|---|---|---|---|---|
| Regression | 5 | $0.16709 \times 10^{8}$ | $0.33417 \times 10^{7}$ | 11.756 | 0.0000 |
| Error | 1458 | $0.41445 \times 10^{9}$ | $0.28426 \times 10^{6}$ | | |
| Total | 1463 | $0.43116 \times 10^{9}$ | | | |

$R^2 = 0.03875$

Juan de Fuca

| Variable | Coefficient | *t*-statistic | Probability |
|---|---|---|---|
| Constant | −788.65 | −4.4216 | 0.0000 |
| Year built | 3.2568 | 2.1538 | 0.0317 |
| Estimate value | $0.35318 \times 10^{-2}$ | 0.16142 | 0.8718 |
| Horsepower | 0.24777 | 0.96256 | 0.3362 |
| Length | $0.63028 \times 10^{-1}$ | 1.9726 | 0.0490 |
| Gross tonnage | 2.1373 | −2.0302 | 0.0428 |

| Source | df | Sum of squares | Mean square | *F*-statistic | Probability |
|---|---|---|---|---|---|
| Regression | 5 | $0.15344 \times 10^{8}$ | $0.30687 \times 10^{7}$ | 16.523 | 0.0000 |
| Error | 600 | $0.11144 \times 10^{9}$ | $0.18573 \times 10^{6}$ | | |
| Total | 605 | $0.12678 \times 10^{9}$ | | | |

$R^2 = 0.12102$

related: the skipper recruits the crew and controls the net. In order to assess the contributions of these components to catch, we perform one-way ANOVA on performance for the two fishing areas; the vessel is the treatment. Only vessels fishing all five years are included. The results are presented in Table 4. The variance components analysis shows that the vessel effect explains 34% of the variance in Johnstone Strait and 29% in Juan de Fuca. The remaining 66–71% of the variability in catch is unexplained and may be attributed to random chance.

If we accept that about one third of the variation in performance is explained by the vessel effect, and only 4–11% of the total variation is explainable by vessel attributes, we have an aggregate picture of 66% unexplained, 10% vessel attributes, and 24% vessel related but not attributes and therefore presumably skipper-, crew-, and net-related. Since skippers may have changed vessels, and in fact did on company boats, we are probably underestimating the skipper component. The aggregate picture is shown in Fig. 3.

We can examine the question of area specialization using an ANOVA similar to that of equation (1), but using our performance index (equation (2)) instead of catch. The weeks of equation (1) become years. To reduce the problems of non-orthogonality further, we only include boats that fished in both areas in the same year. The results of this analysis are presented in Table 5. Note that year, vessel–year, and year–area interactions are not significant. This result is expected, since the

FIG. 3. Determinants of catching power in British Columbia salmon purse seiners.

TABLE 4. ANOVA for vessel performance in Johnstone Strait and Juan de Fuca. Vessel is the treatment. Only vessels fishing all five years included.

Johnstone Strait

| Source | df | Sum of squares | Mean square | *F*-statistic | Probability |
|---|---|---|---|---|---|
| Vessel | 190 | $0.69616 \times 10^8$ | $0.36640 \times 10^6$ | 2.6372 | 0.0000 |
| Residual | 417 | $0.57936 \times 10^8$ | $0.13893 \times 10^6$ | | |
| Total | 607 | $0.12755 \times 10^9$ | | | |

Variance components analysis: % variance among = 34%

Juan de Fuca

| Source | df | Sum of squares | Mean square | *F*-statistic | Probability |
|---|---|---|---|---|---|
| Vessel | 337 | $0.19827 \times 10^9$ | $0.58834 \times 10^6$ | 2.8299 | 0.0000 |
| Residual | 1157 | $0.24054 \times 10^9$ | $0.20790 \times 10^6$ | | |
| Total | 1494 | $0.43881 \times 10^9$ | | | |

Variance components analysis: % variance among = 29%

TABLE 5. ANOVA for vessel performance to examine for interaction between vessels and area. Only vessels fishing both Johnstone Strait and Juan de Fuca included.

| Source | df | Sum of squares | Mean square | *F*-statistic | Probability |
|---|---|---|---|---|---|
| Vessel | 282 | $9.6 \times 10^7$ | $3.4 \times 10^5$ | 2.2 | 0 |
| Area | 1 | $0.27 \times 10^7$ | $27 \times 10^5$ | 17.8 | 0.0001 |
| Vessel–area | 282 | $7.8 \times 10^7$ | $2.8 \times 10^5$ | 1.79 | 0 |
| Residual | 694 | $10.7 \times 10^7$ | $1.5 \times 10^5$ | | |
| Total | 1259 | $28.4 \times 10^7$ | | | |

averages for both factors are zero by our definition of performance. However, since we are dealing with a subpopulation of the total fleet in this analysis (only boats fishing both areas in the same year), differences would occur if this subpopulation were different from the entire population. Having rejected the year, vessel–year, and year–area interactions, we combine them with the residual error to form the final ANOVA table shown at the bottom of Table 5. The picture that emerges from this ANOVA is similar to the separate analyses for Johnstone Strait and Juan de Fuca, but two thirds of the sum of squares are explained by the vessel effect. This analysis permits us to separate the basic differences between vessels in average performance, the vessel sum of squares, from the area specialization shown by the vessel–area interaction. The area specialization accounts for roughly one quarter of the overall variation; non-area-specific differences between vessels account for another one third of overall variation.

## Discussion

Our results suggest that skipper skill and motivation are major determinants in catching power, but this is only by inference. We must find a fishery where information on skippers can be related to catch and vessel performance. Such data will be most useful when there is movement of skippers between vessels: if all skippers stay with the same vessels, we cannot assess the skipper–vessel interaction. The first priority is to find fisheries where skipper information is available.

In Table 3, it appears that vessel attributes in Juan de Fuca account for more of the variance in vessel performance than the attributes in Johnstone Strait. Conversely, from Table 4, the vessel effect may be more pronounced in Johnstone Strait than in Juan de Fuca. The characteristics of these fisheries support our speculation. The limited number of access points and the long line-ups in Juan de Fuca should interfere with skill and motivation components. Furthermore, the rough water is more easily negotiated by large modern boats, and size enables the skipper to set for fish rather than for sea conditions. The Johnstone Strait fishery is characterized by a large number of fishing spots and intense tidal influences that free skippers to adopt a wide range of fishing strategies. Catches may reflect a high degree of motivation and a relative lack of skill. D. Cruickshank (Fleet Rationalization Committee Report, unpubl.) surveyed confidential accountants' records and found that the skippers possessing the largest gross income in his sample also incurred higher expenses resulting in low net incomes relative to vessels ranked lower in catching power. Cove (1973) noted that some captains did not care what their absolute catch was as long as they caught relatively more than other skippers. This attitude and input of young, technologically oriented skippers has resulted in a maximization of the number of sets strategy and an increase in the costs for fishing. Younger skippers have admitted that they have substituted hard, continuous labor for detailed knowledge concerning tides and fish behavior. Company bonuses based on production reinforce this attitude.

Area specialization does exist; many vessels consistently do well in one area and not the other. This result explains in part an unanswered question presented in our study of seine boat mobility (Hilborn and Ledbetter 1979). In that paper, we showed that catches were consistently higher in Juan de Fuca

than in Johnstone Strait. There is no evidence to suggest that differential costs of fishing can account for these differences and we suggested that Juan de Fuca was a less desirable fishery and that fishermen would trade off income for desirable fishing location. Juan de Fuca typically averaged 50% higher in landed value per week than Johnstone Strait. Fishermen suggested that this disparity is caused by area specialization. The skippers were asked why they did not move to Juan de Fuca if they could be making $3000 per week there and only $2000 per week in Johnstone Strait. The fishermen responded that, being a Johnstone Strait fisherman, they would not make the average of $3000 per week if they moved to Juan de Fuca, but because of lack of local knowledge could make less than average. Given true area specialization, this appears to be a good short-term argument: boats that move will not catch the average. Therefore, the disparity in catch per week between the two areas is attributed to a disparity in area knowledge as well as individual preference.

The next question is why do more people not acquire the skill to fish Juan de Fuca? If a fisherman is going to learn to fish in one area, why not learn to fish where it pays best? We believe that a simple answer exists: while Juan de Fuca may pay better on an average weekly basis, the value of learning to fish a given area also depends on the length of the fishing season in an area. The Juan de Fuca fishery is much shorter than the Johnstone Strait fishery. Also, the Juan de Fuca fishery requires a larger, outside net (an extra expense, since all boats possess the smaller, inside net) and a power skiff. Furthermore, Johnstone Strait fishermen are closer to the central and north coast fishing areas. New fishermen unconsciously or consciously learning area-specific skills may well perform a sophisticated total income optimization.

Admittedly, many of the Johnstone Strait specialists reside in the local communities of Alert Bay, Port Hardy, Sointoulla, and Campbell River, so that our previous argument about liking to be close to home is also true. Nevertheless, a major portion of the seine fleet moves up and down the coast, and many of these vessels obviously choose to specialize in areas that per week do not pay so well as Juan de Fuca.

The role of skippers in determining catching power has significant implications for vessel buy back schemes that have operated in British Columbia and have been proposed by the Pearse Commission (Pearse 1982). Some buy back schemes have recognized that there are differences between vessels in the fleet and have operated on a price per ton. The concerns that half of the fleet can be bought out, and yet 80% of the catching power will still remain, are typically centered around the fear of buying out old boats and leaving the new ones. If the determinant of catching power is the skipper and not the physical attributes of the vessel he operates, a buy back of vessels that contribute to production will not reduce catching power.

Accepting the lack of importance of physical attributes, we must believe that the large sums spent on new vessels were not related to catching power for salmon. These expenditures were either directed towards the roe-herring fishery, ways to avoid tax payments, or simply investment in comfort and prestige. If we wish to avoid the further investment of fishing profits in unproductive capital, our new perspective on catching power indicates that the old small vessels should be bought out because these vessels have the potential to absorb significant investments in gear improvement. Under such a buy back, there will be no illusion that the catching power of the fleet is being reduced or that the fishermen remaining in the fishery will have more fish to catch. The rationale for such a buy back is to reduce the potential for future capital investment in these vessels.

Additionally, a landing tax may reduce the number of highly motivated, yet unskilled skippers or force them to adopt a more conservative attitude closely linked to return on investment. Although highly skilled skippers who expend relatively little energy catching large quantities of fish will remain in the fishery, the catching power of the fleet may subside as younger skippers focus on cutting expenses by concentrating on skill rather than motivation and investment.

As a final point for discussion, the elimination of physical attributes as significant determinants in the British Columbia salmon purse seine fleet may not apply to other fisheries (see Pálsson and Durrenberger 1982). Fishermen have suggested that the development of new vessels in the 1973–77 period was not directed towards increased salmon catching power but towards roe-herring catching power. In addition, the British Columbia purse seine fleet for all its diversity is a relatively homogeneous fleet. These vessels are all drum seine boats operating similar nets, with lengths generally between 15 and 25 m. The traditional fisheries whose attributes have been examined show much more diversity in the fleets. However, as vessels become more physically homogeneous, catching power may continue to change, and the determinants of the change will be use of information rather than physical attributes. The British Columbia purse seine fishermen who do well are those who have local knowledge and are smarter. They collect and use information more efficiently. Recent work on the efficiency of search (Mangel and Clark 1983) suggests that considerable improvements can be made in fishing efficiency solely by improving information utilization. We suspect that major improvements in information processing could lead to significant increases in vessel efficiency that will be quite difficult to document.

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## References

Cove, J. J. 1973. Hunters, trappers and gatherers of the sea: a comparative study of fishing strategies. J. Fish. Res. Board Can. 30: 249–259.

Hilborn, R., and M. Ledbetter. 1979. Analysis of the British Columbia salmon purse seine fleet: dynamics of movement. J. Fish. Res. Board Can. 36: 384–391.

Mangel, M., and C. W. Clark. 1983. Uncertainty, search, and information in fisheries. J. Cons. Int. Explor. Mer 41: 93–103.

Pálsson, G., and P. Durrenberger. 1982. To dream of fish: the causes of Icelandic skippers' fishing success. J. Anthropol. Res. 227–242.

Pearse, P. H. 1982. Turning the tide: a new policy for Canada's Pacific fisheries. Report of the Royal Commission on Pacific Fisheries Policy. Ministry of Supplies and Services, Ottawa, Ont. 292 p.

Pope, J. A. [ed.] 1975. Measurement of fishing effort. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 168: 102 p.

# Assessing Significance of Physiological Differences among Three Esocids with a Bioenergetics Model

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To predict stocking success of esocids in Ohio waters with different thermal regimes, we measured individual food consumption, conversion efficiency, growth, and metabolic rate for Ohio stocks of northern pike (*Esox lucius*), muskellunge (*E. masquinongy*), and their hybrid, tiger muskellunge, in laboratory experiments. The first three parameters were quantified during 2-wk experiments of ad libitum feeding on fathead minnows (*Pimephales promelas*) at seven constant temperatures (5, 15, 20, 22.5, 25, 27.5, and 30°C). The food consumption and growth data suggest that northern pike should grow faster than muskellunge at cool temperatures (≤20°C), but slower than muskellunge at warm temperatures (>25°C). Latitudinal differences in their natural distributions might explain this observation. Growth data of the hybrid showed no such obvious relationship to either of the parents. Metabolic rates were determined by measuring oxygen consumption in a closed, static respirometer at five constant temperatures (5, 15, 20, 25, and 30°C). We found little difference in metabolic rates among the three taxa. To examine these data further, we used a bioenergetics model that simulated different stocking conditions, both natural (thermal regime and prey availability) and human controlled (stocking size and date). With this model, we predicted growth for 12–15 mo after stocking. In general, summer-stocked fish were about 35–90% larger 15 mo after stocking than were fall-stocked fish 12 mo after stocking. More specifically, the combined effect of ration and temperature permitted hybrids to grow faster than the parents in all simulations. Northern pike grew larger than muskellunge in a cool system, but smaller than muskellunge in a warm system with summer stocking. Based on bioenergetic considerations, tiger muskellunge should outgrow both northern pike and muskellunge in thermal regimes common to Ohio waters.

Pour déterminer le succès de l'ensemencement d'esocidés dans des cours d'eau de différentes températures en Ohio, nous avons mesuré la consommation d'éléments nutritifs et leur transformation, le taux de croissance et le métabolisme du brochet (*Esox lucius*), du maskinongé (*E. masquinongy*) et de l'hybride résultant du croisement de ces deux espèces, en étudiant en laboratoire des sujets prélevés dans les stocks de l'Ohio. Nous avons quantifié les trois premiers paramètres mentionnés ci-dessus en étudiant pendant 2 sem des têtes-de-boules (*Pimephales promelas*) nourries à volonté et conservées à sept températures différentes (5, 15, 20, 22,5, 25, 27,5 et 30°C). D'après les résultats que nous avons obtenus sur la consommation de nourriture et la croissance, le brochet devrait se développer plus rapidement que le maskinongé en eau froide (≤20°C) et plus lentement en eau chaude (>25°C). Ce phénomène s'explique peut-être par la différence de latitude qu'il y a entre l'aire de distribution naturelle de ces deux espèces. Par ailleurs, les données que nous possédons sur la croissance de l'hybride ne révèlent aucune relation évidente avec l'un ou l'autre des parents. Nous avons évalué le métabolisme en mesurant la consommation d'oxygène dans un respiromètre statique fermé, à cinq températures différentes (5, 15, 20, 25 et 30°C) ; il y avait peu de différence entre les trois poissons. Pour pousser l'analyse, nous nous sommes servi d'un modèle représentant les processus bioénergétiques avec lequel nous avons simulé différentes conditions d'ensemencement mettant en jeu des facteurs naturels (température de l'eau et abondance des proies) et des éléments sous contrôle (nombre de poissons ensemencés et date de l'opération). Nous avons ainsi pu prévoir la croissance des poissons durant les 12 ou 15 mo suivant l'ensemencement. En général, les poissons ensemencés en été étaient de 35 à 90 % plus gros au bout de 15 mo que les poissons ensemencés en automne, au bout de 12 mo. Plus précisément, nous avons constaté qu'en raison de l'effet combiné de la ration et de la température, les hybrides se développent plus rapidement que les poissons parents, quelles

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que soient les conditions. Le brochet devient plus gros que le maskinongé en eau froide, mais il demeure plus petit en eau chaude lorsque l'ensemencement a lieu en été. D'après nos données sur les processus bioénergétiques, l'hybride devrait se développer mieux que ses parents à la température des eaux qu'on trouve généralement en Ohio.

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Northern pike (*Esox lucius*) and muskellunge (*E. masquinongy*) have been stocked beyond their natural ranges for nearly 100 yr to provide trophy fisheries across the United States (Webster et al. 1978). Within the last 20 yr the hybrid, tiger muskellunge (male northern pike × female muskellunge), also has been stocked into lakes and reservoirs. Hybrids have been chosen over their parents because of hatchery-related benefits (Hesser 1978); relative to their parents, hybrids exhibit (1) greater survival through hatching, (2) greater disease resistance, and (3) the ability to feed readily on dry food (a definite economic advantage). Though the hybrid has these rearing advantages, their survival after stocking has often been quite low (Stein et al. 1981). Thus, to decide which of these esocids should be stocked, information related to poststocking survival must be gathered for each taxon.

Previous comparative studies on thermal tolerance (Bonin and Spotilla 1978; Scott 1964), growth rates (Weithman and Anderson 1977), and conversion efficiencies of esocids in laboratory and pond experiments suggest that abiotic factors (particularly temperature) affect northern pike, muskellunge, and tiger muskellunge differently. In three small impoundments in West Virginia, Hess (1981) found that tiger muskellunge grew faster than muskellunge in one lake, muskellunge and northern pike grew similarly in a second, and all three taxa grew similarly in a third lake. These studies demonstrate how different situations might favor different taxa, but they do not provide the mechanisms for such; therefore, it is nearly impossible to predict which taxon would do best in a particular system.

The problem is twofold. First, a multiplicity of variables, most notably temperature and ration, interact to determine growth. Therefore, it is not always clear why a single taxon grows well (or poorly) in a given system. Second, the interaction of ration and temperature probably differs among the three taxa. An efficient means of examining this complex problem is mathematical modeling. Bioenergetics models that summarize the unique physiological responses of different fishes to ration and temperature allow investigators to take into account both the effects of ration and temperature on individual fishes and the differences between fishes. Bioenergetics models, as an aid to field research, previously have been used to examine growth of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) (Kitchell et al. 1977), largemouth bass (*Micropterus salmoides*) (Cochran and Rice 1982; Rice et al. 1983), and sea lampreys (*Petromyzon marinus*) (Kitchell and Breck 1980). Determining system characteristics that favor each esocid is critical, because maintaining a tiger muskellunge stocking program also requires adult northern pike and muskellunge. However, investigators will not fully understand results from field experiments until some of the physiological factors that contribute to those results are defined and understood. Therefore, our first objective was to determine differences in metabolism, food consumption, conversion efficiency, and growth among northern pike, muskellunge, and tiger muskellunge as a function of temperature, and summarize these data in a bioenergetics model for each taxon. This approach uses a simple mass balance equation where caloric intake is equal to all energetic costs plus growth. Taxon-specific functions for food consumption and metabolism were incorporated into the model with the assumption that these experimental values approximated field values.

We expected to find physiological differences related to temperature between northern pike and muskellunge because of latitudinal differences in their natural distributions. Northern pike extend north to the Arctic Circle and south into central Ohio, whereas muskellunge extend north only to southern Canada and south to Tennessee (Crossman 1978). Although field data are available that compare hybrid growth with that of its parents, these data are only loosely connected with temperature. One hypothesis suggests that the hybrid reaction to a range of temperatures would be intermediate to both parents. Alternatively, hybrid vigor could permit tiger muskellunge to grow more efficiently than its parents (Scott 1964; Pecor 1978).

The second objective of this study was to use the bioenergetics model to assess the significance of differences among these three taxa as they relate to stocking options and thermal environments. When planning stocking strategies, managers might have data on the thermal regimes of lakes they wish to stock and might be flexible in choosing fish species, stocking size, and stocking date. By modelling growth of each esocid with different thermal regimes, stocking dates, and size at stocking, we can compare directly the success of each taxon in different environments.

## Materials and Methods

### Fish stocks

Young-of-year northern pike, muskellunge, and tiger muskellunge were obtained from Ohio Division of Wildlife fish farms at St. Marys, London, and Kincaid, respectively. The northern pike stock originated from Lake Erie and has been maintained in hatchery ponds at St. Marys (Auglaize County) since initial collection over 25 yr ago. The Ohio muskellunge stock originated from Ohio River tributaries in southern Ohio and has been maintained in Ohio reservoirs for over 25 yr. Muskellunge of the Ohio River drainage system are recognized as a subspecies, *E. m. ohioensis*, separate from more northern stocks (Trautman 1957). The tiger muskellunge used in these experiments were products of male northern pike (originally from St. Marys fish farm) collected from Lake Rupert (Vinton County) and female muskellunge collected from Rocky Fork Lake (Highland County). All three taxa were held in 400-L aquaria at 10–20°C until they were used in experiments.

### Metabolic Rate Experiments

Oxygen consumption, as a measurement of metabolic rate, was measured with a closed, static respirometer, which consisted of a round 4.68-L tank with a clear Plexiglas cover (sealed

with stopcock grease) and was immersed in a constant-temperature (5, 15, 20, 25, or 30°C) water bath. The oxygen probe from a Beckman model 0260 oxygen ($O_2$) analyzer fit through a hole in the Plexiglas; a magnetic stirrer on top of the chamber circulated water. Output from the oxygen analyzer was monitored continuously with a chart recorder. Records were digitized with a Hewlett-Packard model 9825B computer and a model 9874A digitizer to determine the initial and final dissolved oxygen (DO) content of the water, and then the amount of oxygen consumed per gram of fish per hour was determined. Rate of metabolism was derived from oxygen consumption by converting mg $O_2 \cdot g^{-1} \cdot h^{-1}$ to $g \cdot g^{-1} \cdot d^{-1}$ with an oxycalorific coefficient of 3.24 cal·mg $0_2^{-1}$ (Elliott and Davidson 1975) and a fish caloric value of 860 $cal \cdot g^{-1}$ (R. Stein, unpubl. data) for use in the model.

Following the suggestions of Brett (1962), we allowed time for the fish to acclimate to temperature and recover from handling. Before experiments, fish were held at test temperatures with a photoperiod of 16 h light : 8 h dark for at least 1 wk (usually 2 wk) and were put in the respirometer 15 h before the experiment. Temperatures were changed slowly ($1–3° \cdot d^{-1}$) when acclimating fish from holding temperature to test temperature. Fish were starved for at least 120, 72, and 24 h for experiments at 5, 15, and ≥20°C, respectively. These periods approximate time of gut evacuation, which we determined for tiger muskellunge at 5, 15, and 25°C (Bevelhimer 1983). At least 30 min before experiments began in the morning, the respirometer water was flushed (with minimal disturbance of the fish) to eliminate overnight accumulation of $CO_2$ or ammonia. Water in the respirometer was aerated continuously except during experiments. Amount of DO at the beginning of a trial depended on the test temperature and usually was between 7.0 and 10.0 $mg \cdot L^{-1}$. Amount of DO at the end of a trial never fell below 5.0 $mg \cdot L^{-1}$. At warm temperatures (>20°C), experiments lasted about 0.75 h, and at cool temperatures (<20°C) about 1–1.5 h was required for adequate measurements of oxygen consumption. At least 13 trials with at least four individuals were performed for each of the three taxa at each temperature. At the end of each experiment, fish were weighed and measured. Total lengths were 128–227 mm; weights were 9.5–53.2 g ($\bar{X}$ = 20.7 g).

To minimize activity, the stirrer was only turned on 5–10 min at the beginning and at the end of each trial to obtain initial and final DO. When the stirrer was off, which was a majority of the time, fish were usually inactive. When a fish was active, its movement tended to stir the water around the oxygen probe causing erratic output on the chart recorder, which could be examined later to determine if a fish had been active. Those trials in which fish were active more than 35% of the time (as determined by periodic observation and/or examination of the chart record) were not included in the analysis.

The metabolic rates determined in these experiments might be best designated as "low routine" metabolism or "uncontrolled standard" metabolism as defined by Beamish and Dickie (1967). Whatever the label, we feel that the respiration rates approximate the metabolism of inactive fish in the field. Costs of activity will be addressed later in the model section.

An equation that expresses respiration rates as an exponential function of weight, and includes the temperature dependence as a form of van't Hoff's $Q_{10}$ rule (Brett and Groves 1979), was determined for each of the three taxa and for all taxa combined:

$$(1) \quad mg\,O_2 \cdot g^{-1} \cdot h^{-1} = a_2 \cdot B^{b_2} \cdot e^{mT}$$

or, in linear form:

$$(2) \quad \ln (mg\,O_2 \cdot g^{-1} \cdot h^{-1}) = \ln (a_2) + b_2 \cdot \ln (B) + mT$$

where $a_2$ is an intercept constant, $b_2$ is the weight-dependent constant, $m$ is the temperature-dependent constant (related to $Q_{10}$ by $Q_{10} = e^{10 \cdot m}$), $B$ (biomass) is wet weight (grams), and $T$ is temperature (degrees Celcius). Because we used a narrow range of sizes (9–53 g), values for $b_2$ could not be determined accurately. Diana (1982) estimated $b_2$ at −0.18 with a larger size range (5–1200 g) of northern pike at 14°C. Because Beamish (1970) suggested that $b_2$ does not change with temperature, we used this value at all temperatures, making the additional assumption that it did not differ among the three taxa. To determine total respiration (mg $O_2 \cdot h^{-1}$), 0.82 ($b_2$ + 1) can be used for the weight coefficient. The constant values, $a_2$ and $m$, were determined with a least squares linear regression procedure, where ln (mg $O_2 \cdot g^{-1} \cdot h^{-1}$) − (−0.18·ln ($B$)) was the dependent variable, and $T$ was the independent variable. Duncan's multiple range test (Helwig and Council 1979) was performed on these data to determine if differences among taxa were substantial enough to warrant three separate equations.

## Food Consumption Experiments

Individual esocids at seven constant temperatures (5, 15, 20, 22.5, 25, 27.5, and 30°C) were fed ad libitum on live fathead minnows (*Pimephales promelas*) that were supplied daily for 14 d. Initial predator lengths were 125–210 mm; initial weights were 7.2–43.5 g ($\bar{X}$ = 19.3 g). Mean sample size was 15 individuals per taxon per temperature for experiments at temperatures ≤25°C and 9 individuals per taxon per temperature for experiments at temperatures >25°C. Laboratory aquaria (29–118 L) were divided so that two or three fish could be tested per tank. Minnow lengths were 25–40% the total length of fish to which they were fed, which corresponded to preferred sizes determined by Gillen et al. (1981). All minnows added to the tank and any dead ones removed were damp dried with a paper towel and weighed to determine the amount of food consumed. After 14 d, remaining minnows were removed, and the esocids were starved for 120, 72, or 24 h for experiments at 5, 15, and ≥20°C, respectively, before final weighing to insure that final weights represented actual growth and not an undigested meal (Bevelhimer 1983). Because prey were eaten every 3–6 d at 5°C instead of daily as at other temperatures, 5°C experiments ended when a fish consumed its first minnow after day 13. Remaining minnows were removed, and fish were starved for 120 h before final weighing. Thus, 5°C experiments ranged from 14 to 20 d, but bias (overestimated final weights) due to different amounts of food in the stomach was prevented.

Maximum consumption rate ($C_{max}$, g food consumed·g $fish^{-1} \cdot d^{-1}$), gross conversion efficiency (change in g wet weight·g food $consumed^{-1}$), and relative growth (change in g wet weight·g mean $weight^{-1} \cdot d^{-1}$) were calculated for each fish (note: mean weight is an arithmetic mean of initial and final weights). Energy content of the esocids and the fathead minnows did not differ; mean energy content of both was 860 $cal \cdot g^{-1}$ (R. Stein, unpubl. data). Energy content of fishes does vary with season (Diana and Mackay 1979; Pierce et al. 1980), but sufficient data for juvenile esocids or fathead minnows were not available to quantify specific seasonal differences.

After trying different types of equations (i.e. second, third, fourth, and fifth order, and log–log and semi-log transformations), we decided that a third-order polynomial equation best

reflected the dependence of food consumption on weight and temperature:

$$(3) \quad C_{max}(g \cdot g^{-1} \cdot d^{-1}) = a_1 \cdot B^{b1} \cdot e^{(xT + yT^2 + zT^3)}$$

or, in linear form:

$$(4) \quad \ln C_{max} = \ln (a_1) + b_1 \cdot \ln (B) + xT + yT^2 + zT^3$$

where $a_1$ is an intercept constant, $x$, $y$, and $z$ are taxon-specific temperature-dependent constants, $b_1$ is a weight-dependent constant, $B$ is wet weight (grams), and $T$ is temperature (degrees Celcius). Because the literature contains no values of $b_1$ for esocids, and we could not accurately determine it with our data, we assumed that $b_1 = b_2 = -0.18$. Although Brett and Groves (1979) indicated no reason why $b_1$ should equal $b_2$, it was convenient for this study. This value provided food consumption rates for large fish (up to 1000 g) that we felt were realistic, based on growth of juvenile tiger muskellunge in a small impoundment (Stein et al. 1982). The taxon-specific constants ($a_1$, $x$, $y$, and $z$) were determined with a least squares linear regression procedure with $\ln (C_{max}) - (-0.18 \cdot \ln (B))$ as the dependent variable, and $T$, $T^2$, and $T^3$ as independent variables. Duncan's multiple range test was performed on these data to determine if differences among taxa were substantial enough to warrant three separate equations.

## Model

### Basic Components

Specific growth of juvenile esocids can be calculated with an equation similar to that used by Kitchell et al. (1977) for yellow perch:

$$(5) \quad G = C - (M + F + U)$$

where

$G$ = specific growth rate ($g \cdot g^{-1} \cdot d^{-1}$), C = specific rate of food consumption, $M$ = specific rate of metabolism, which includes inactive, active, and specific dynamic action (SDA) components, $F$ = specific rate of egestion, and $U$ = specific rate of excretion.

Each of the terms of this equation will be dealt with separately in the following descriptions.

*Consumption*

Specific rate of consumption was determined by the equation

$$(6) \quad C(g \cdot g^{-1} \cdot d^{-1}) = C_{max} \cdot P$$

where $C_{max}$ (eq. 3) is the maximum rate at a particular temperature for each taxa, and $P$ is a proportional constant indicating the proportion of $C_{max}$ actually consumed.

*Metabolism*

The total cost of metabolism includes the increase above standard metabolism due to increased activity and the cost of processing and assimilating food. The following factors were incorporated with the basic metabolic rate equation (eq. 1) to determine the additional cost of activity: direct relationship of swimming speed to increase in oxygen consumption (Wohlschlag and Juliano 1959; Brett 1965); burst-speed swimming (Webb 1977); cruise-speed swimming (Diana 1980); amount of daily activity at cruising speed (Diana 1980); the daily duration of burst-speed swimming based on duration of burst-speed swimming per feeding bout (Moody et al. 1983); and the number of feeding bouts per day (Bevelhimer 1983). The first factor, the relation of swimming speed to increased oxygen consumption, has not been computed for esocids, so this could be a source of error. Throughout these computations, we assumed that the three taxa did not differ in activity or swimming speeds. With activity durations and swimming speeds constant across size, temperature, and taxon, the inclusion of the activity factor increases the metabolic rate by 13% over the standard metabolic rate. For a more detailed explanation, see Bevelhimer (1983).

The cost of processing and assimilating food (specific dynamic action (SDA)) was assumed to be a constant proportion ($S$) of food consumption ($C$).

$$(7) \quad SDA(g \cdot g^{-1} \cdot d^{-1}) = S \cdot C.$$

Jobling (1981) suggested that $S$ varies with ration (quality and quantity) and temperature; however, for the sake of simplicity and the lack of specific values for esocids, we chose to use an average value suggested by Brett and Groves (1979) for all fishes, $S = 0.14$. Therefore, the total metabolic cost can be determined by the following equation:

$$(8) \quad M(g \cdot g^{-1} \cdot d^{-1}) = 1.13 \cdot (a_2 \cdot B^{b_2} \cdot e^{mT}) + 0.14 \cdot C.$$

For use in the bioenergetics model, the intercept value $a_2$ was converted from mg $O_2 \cdot g^{-1} \cdot h^{-1}$ to $g \cdot g^{-1} \cdot d^{-1}$ by multiplying $a_2 \cdot (3.24$ cal $\cdot$ mg $O_2^{-1}) \cdot (1$ g $\cdot 860$ cal$^{-1}) \cdot (24$ h $\cdot$ d$^{-1})$.

*Egestion and excretion*

Energy losses from egestion ($F$, feces) and excretion ($U$, urea and other nitrogenous wastes) were assumed to be constant proportions of consumption ($C$) expressed by the equations

$$(9) \quad F(g \cdot g^{-1} \cdot d^{-1}) = f \cdot C,$$

where $f$ is the proportion of food consumed that is egested and

$$(10) \quad U(g \cdot g^{-1} \cdot d^{-1}) = u \cdot C,$$

where $u$ is the proportion of food consumed that is excreted.

No data were available for egestion ($f$) or excretion ($u$) for esocids; hence, we chose to use constant values of $f$ (0.20) and $u$ (0.07) as suggested by Brett and Groves (1979), who averaged values from a variety of fishes. Egestion and excretion rates may vary substantially with ration and temperature (Elliott 1976), but the combination of decreasing egestion losses and increasing excretion losses with increasing temperature produces a combined effect that varies little across temperature (Kitchell et al. 1977). Symbols and values of all model parameters discussed in this section are summarized in Table 1.

### Variable Components

The model includes variables that were useful in simulating different stocking options, such as time of stocking, fish size at stocking, and choice of lakes (differing in thermal regime). We chose two stocking dates, one in summer and one in fall, that were typical of actual stocking dates in Ohio: day 180 (June 29) and day 270 (September 27). All simulations ended on September 27 of the second year; thus, simulations of summer stocking ran 15 mo whereas those for fall ran 12 mo. Typical sizes at the stocking dates were 9 g (125 mm) in summer and 80 g (250 mm) in fall, though fall sizes can be manipulated by hatchery managers to produce fish smaller or larger than 80 g.

Two annual thermal regimes were incorporated in the model to evaluate the importance of temperature on growth. Temperatures from 1 m deep at Caesar Creek Lake (1980) in southwestern Ohio represented a thermal regime typical of Ohio

TABLE 1. Symbols, definitions, and parameter values used for simulating growth of northern pike (NP), muskellunge (M), and tiger muskellunge (TM).

| Equation | Symbol | | Parameter description | Value | Standard error | Source[a] |
|---|---|---|---|---|---|---|
| Metabolism | | | | | | |
| 1 | $a_2$ | | Intercept coefficient | 0.1025 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ or $9.27 \times 10^{-3}$ $g \cdot g^{-1} \cdot d^{-1}$ | +0.0062, −0.0059[b] +$0.56 \times 10^{-3}$, −$0.54 \times 10^{-3}$[b] | 3 |
| 1 | $b_2$ | | Weight-dependent exponent | −0.18 | ±0.05[c] | 2 |
| 1 | $m$ | | Temperature-dependent exponent | 0.055 | ±0.003 | 3 |
| 10 | $S$ | | Specific dynamic action factor | 0.14 | | 1 |
| Food consumption | | | | | | |
| 3 | $a_1$ | (NP) | Intercept coefficient | $2.44 \times 10^{-2}$ $g \cdot g^{-1} \cdot d^{-1}$ | +$0.81 \times 10^{-2}$, −$0.61 \times 10^{-2}$[b] | 3 |
| | | (M) | Intercept coefficient | $1.26 \times 10^{-2}$ $g \cdot g^{-1} \cdot d^{-1}$ | +$0.32 \times 10^{-2}$, −$0.25 \times 10^{-2}$[b] | |
| | | (TM) | Intercept coefficient | $4.60 \times 10^{-3}$ $g \cdot g^{-1} \cdot d^{-1}$ | +$1.29 \times 10^{-3}$, −$1.01 \times 10^{-3}$[b] | |
| 3 | $b_1$ | | Weight-dependent exponent | −0.18 | | 3 |
| 3 | $x$ | (NP) | Temperature-dependent exponent | −0.024 | ±0.070 | 3 |
| | | (M) | Temperature-dependent exponent | 0.060 | ±0.057 | |
| | | (TM) | Temperature-dependent exponent | 0.401 | ±0.060 | |
| 3 | $y$ | (NP) | Temperature-dependent exponent | $1.25 \times 10^{-2}$ | ±$0.45 \times 10^{-2}$ | 3 |
| | | (M) | Temperature-dependent exponent | $0.75 \times 10^{-2}$ | ±$0.37 \times 10^{-2}$ | |
| | | (TM) | Temperature-dependent exponent | −$1.40 \times 10^{-2}$ | ±$0.38 \times 10^{-2}$ | |
| 3 | $z$ | (NP) | Temperature-dependent exponent | −$3.26 \times 10^{-4}$ | ±$0.86 \times 10^{-4}$ | 3 |
| | | (M) | Temperature-dependent exponent | −$2.16 \times 10^{-4}$ | ±$0.69 \times 10^{-4}$ | |
| | | (TM) | Temperature-dependent exponent | $1.55 \times 10^{-4}$ | ±$0.72 \times 10^{-4}$ | |
| 11 | $f$ | | Egestion factor | 0.20 | | 1 |
| 12 | $u$ | | Excretion factor | 0.07 | | 1 |

[a]Parameter sources: 1, Brett and Groves (1979); 2, Diana (1982); 3, derived in this study.
[b]Plus and minus errors differ because this coefficient was determined with logarithmic transformation.
[c]95% confidence limits (Diana 1982).

impoundments. Water temperatures were not measured during the winter at Caesar Creek Lake, so we assumed the temperature was 2°C when the lake was ice-covered. For a contrasting temperature regime, we obtained daily temperatures from 6–7 m deep at Alum Creek Lake (1981) in central Ohio. Although oxygen is usually available at 6–7 m deep in Alum Creek Lake, this condition is atypical of Ohio impoundments during summer. However, this thermal regime will be useful for examining the response of the three esocids to different annual temperature regimes (henceforth known as warm, Caesar Creek Lake and cool, Alum Creek Lake, illustrated in Fig. 1).

Evidence from radio telemetry studies (Headrick et al. 1982) suggests that northern pike regulate their body temperatures by moving to those available water temperatures that are more conducive to efficient growth. We simulated the effects of behavioral thermoregulation by permitting each esocid to seek its optimal temperature for growth (as determined in growth simulations at constant temperatures and maximum ration) whenever water temperatures rose above optimal. The warm regime from Caesar Creek Lake was used for these simulations. Temperature could be reduced no more than 4°C, hypothetically, the maximum allowable change in Caesar Creek Lake due to the presence of a thermocline, below which was an anoxic hypolimnion.

We also manipulated ration level (controlled by the value of $P$) to reflect prey availability and seasonal food requirements. Constant levels were established through iteration with the bioenergetics model to produce target weights on December 31 (first year's end) and September 27 (end of simulation) by adjusting the value of $P$. Target weights of 300 g by December 31 and 900 g by September 27 were estimated from average sizes of YOY (about 375 mm) and yearling (about 525 mm) esocids from West Virginia lakes (Hess 1981). Ninety percent of $C_{max}$ ($P = 0.9$) was required to reach target weight by December 31. From January 1 to September 27, 55% of $C_{max}$ ($P = 0.55$) produced average weights of about 900 g.

Based on the constant $P$ values mentioned above and seasonal prey densities from field sampling (Stein et al. 1982), we developed a hypothetical, variable ration scheme to examine the effect of variable ration on seasonal growth. These rations were estimated for immature fish and would probably be inappropriate for adult fish experiencing spawning behavior. The seasonal variation developed for this study and described below was similar to the sine curve projection of the annual available prey cycle presented in fig. 5 of Jenkins (1979).

(1) July–February $P = 0.9$: this ration was required to reach 300 g by December 31; though prey abundance in winter is low, consumption requirements are also low.

(2) March–May $P = 0.4$: prey levels continue to decline, but consumption requirements increase markedly as temperatures warm to 18°C.

(3) June–July $P = 0.55$: the new year class of forage fishes becomes available, but are less than optimal size; consumption requirements are still increasing slightly.

(4) August–September $P = 0.7$: forage fishes are abundant and at optimal sizes; consumption requirements are still high.

Simulations were performed with different combinations of the variable components described above.

## Results

### Metabolic Rate Experiments

Change in metabolic rate as a function of temperature was similar for all three taxa (Fig. 2). No significant differences

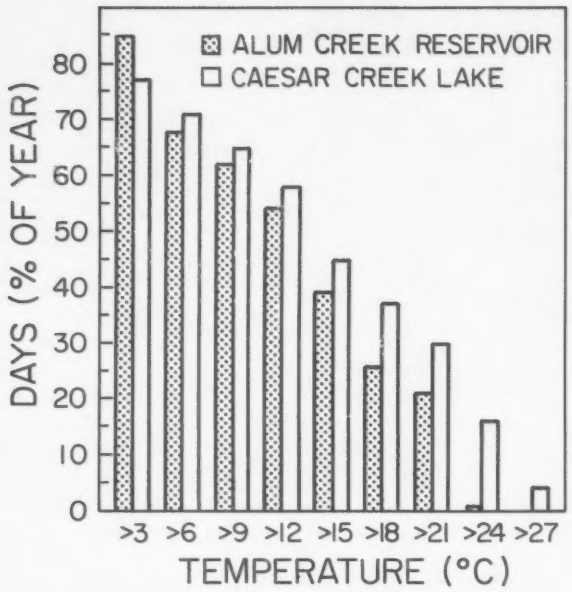


FIG. 1. Comparison of annual temperature regimes from the warm system (Caesar Creek Lake at 1 m) and the cool system (Alum Creek Lake at 6–7 m) that were used in the bioenergetics model.

($\alpha = 0.05$ unless noted otherwise) among taxa existed at 5 or 30°C, and no consistent pattern of significant differences occurred at the other temperatures (Table 2). These results indicate that the hypothesized differences between northern pike and muskellunge with regard to temperature were not evident for metabolic rate. Therefore, a single curve (eq. 1) for all three taxa was fit to all measurements of metabolic rate across temperature (Fig. 2):

$$M(\mathrm{mgO_2 \cdot g^{-1} \cdot h^{-1}}) = (0.1025) \cdot (B^{-0.18}) \cdot (e^{0.055 \cdot T}).$$

The $a_2$ value becomes $9.27 \times 10^{-3}\ \mathrm{g \cdot g^{-1} \cdot d^{-1}}$ when used in the bioenergetics model. The $m$ value of 0.055 corresponds to a $Q_{10}$ of 1.73. The logarithmic transformation that was used to generate this curve introduced a bias (Beauchamp and Olson 1973) which can be corrected by multiplying the result by a correction factor of 1.075. Although we did not include this correction factor, this oversight should have little effect on the modelling results, because it affected all taxa equally.

## Food Consumption Experiments

Using an analysis of covariance procedure, we determined that there was a significant taxa–temperature interaction with regard to food consumption. To examine this interaction more closely, Duncan's multiple range test was used to document differences in mean consumption rates among taxa at each temperature (Table 2). At cool temperatures, 5 and 20°C, northern pike consumption was significantly greater than muskellunge (at 15°C the northern pike consumption was also greater than the muskellunge's, but not significantly so), and at warm temperatures, 27.5 and 30°C, muskellunge consumption was significantly greater than northern pike's. This supports the hypothesized difference between northern pike and muskellunge with regard to temperature. For the above reasons we chose to fit separate curves (eq. 3) to the food consumption data for each taxon (Fig. 3). These equations were included in the bioenergetics model to provide estimates of maximum food consumption rates at any temperature (Table 1). Caution should be taken when applying these equations to temperatures outside the range of our experimental temperatures (5–30°C). The optimum temperature for consumption can be calculated by differentiating equation 3 and finding the $T$ that provides a result of zero. These temperatures were 24.6, 26.7, and 23.5°C for northern pike, muskellunge, and tiger muskellunge respectively.

We also examined the differences in both conversion efficiency and growth among the three taxa (Table 2). The most noteworthy differences in conversion efficiency occurred at 5°C where northern pike were more efficient than muskellunge and the hybrid, and at 30°C where northern pike were less efficient than muskellunge or the hybrid. Generally, the most efficient temperatures for all three fishes were 20 and 22.5°C. Comparisons among means at different temperatures for each fish revealed that maximum efficiency occurred at a plateau across several temperatures. No differences existed among values from 20 to 27.5°C for both northern pike and muskellunge; conversion efficiency of the hybrid was highest between 15 and 22.5°C. The experimental method at 5°C (120-h starvation before weighing) may have resulted in conversion efficiency values lower than actual.

Differences in growth rates display trends that were similar to those found for food consumption and conversion efficiency. At 5°C northern pike grew faster than muskellunge or tiger muskellunge. Growth rates at 5°C for all three taxa may be lower than actual because of the methods used for 5°C. At 15°C the hybrid had greater growth than either of the parent species; hybrid growth was also fastest at 20 and 22.5°C, but not significantly so. By 25°C, growth rate of the hybrid had drastically decreased, so much so that hybrid growth was significantly slower than the parents' at both 25 and 27.5°C. As temperatures increased, the growth rate of the hybrid began decreasing at a cooler temperature than either parent. However, the decrease did not continue through 30°C as it did with northern pike, but leveled off such that hybrid growth rates were similar to those of muskellunge at 30°C, both significantly greater than the northern pike's.

## Predicted Versus Observed Growth Rate

To test the accuracy of the model derived from these experiments, simulations of the 2-wk food consumption experiments were run at the seven experimental temperatures with $P = 1.0$ to simulate ad libitum feeding. Starting weights for these simulations equalled the mean initial weight for each species at each temperature in experiments. Predicted growth rate was compared with the mean observed growth rate at each temperature for each taxon (Fig. 4). In all but two cases (northern pike and muskellunge at 5°C), predicted values were within one standard deviation of observed means. For all of the taxa, predicted values were neither consistently higher nor lower than observed values across temperature, suggesting that the 41% subtracted for SDA (14%), egestion (20%), and excretion (7%) was an acceptable approximation; however, accuracy of individual parameters could not be evaluated. For the same 2-wk simulations, the conversion efficiencies were slightly higher than those determined experimentally, which suggests that the actual values for $S$, $u$, and/or $f$ might be a little higher than our estimates.

When simulations were run with the same starting weight (20 g) for all fish at all temperatures and $P = 1.0$, optimal temperatures for growth were 24°C for northern pike, 26°C for

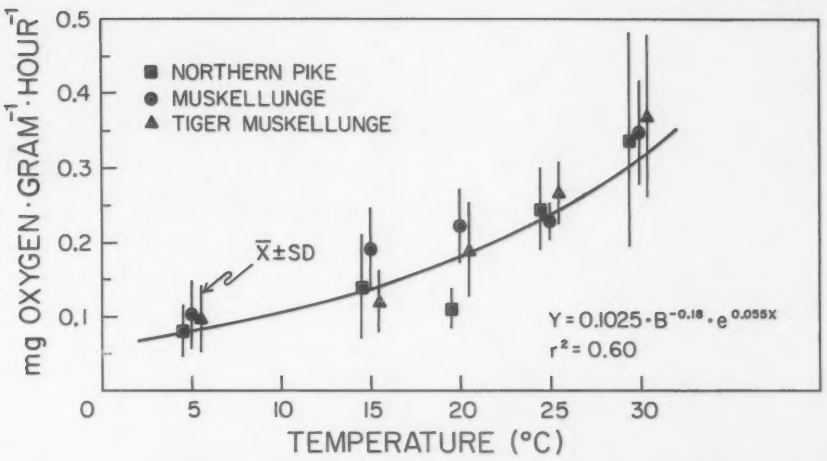


FIG. 2. Mean respiration rates (±1 SD) of northern pike, muskellunge, and tiger muskellunge determined at 5, 15, 20, 25, and 30°C in a closed static respirometer. A single exponential curve (dependent on temperature and weight) was fitted to all data.

TABLE 2. Mean metabolic rates, food consumption rates, gross conversion efficiencies, and relative growth rates at seven experimental temperatures positioned highest to lowest within each temperature. Species is denoted at the right of each value as NP (northern pike), M (muskellunge), or TM (tiger muskellunge). Values connected with vertical bars on the left side are not significantly different ($\alpha = 0.05$) as determined by Duncan's multiple range test (within temperature comparisons only).

| Test temperatures (°C) | | | | | | |
|---|---|---|---|---|---|---|
| 5 | 15 | 20 | 22.5 | 25 | 27.5 | 30 |
| *Metabolic rate (mg $O_2 \cdot g^{-1} \cdot h^{-1}$)* | | | | | | |
| 0.102 M | 0.191 M | 0.222 M | | 0.266 TM | | 0.371 TM |
| 0.097 TM | 0.140 NP | 0.190 TM | | 0.245 NP | | 0.349 M |
| 0.080 NP | 0.120 TM | 0.111 NP | | 0.228 M | | 0.339 NP |
| *Food consumption ($g \cdot g^{-1} \cdot d^{-1}$)* | | | | | | |
| 0.017 TM | 0.080 TM | 0.113 NP | 0.134 TM | 0.122 NP | 0.131 M | 0.127 M |
| 0.017 NP | 0.057 NP | 0.110 TM | 0.125 M | 0.119 M | 0.109 TM | 0.112 TM |
| 0.013 M | 0.052 M | 0.097 M | 0.103 NP | 0.098 TM | 0.108 NP | 0.082 NP |
| *Gross conversion efficiency (g growth·g consumed$^{-1}$)* | | | | | | |
| 0.261 NP | 0.337 TM | 0.368 TM | 0.377 TM | 0.357 M | 0.345 NP | 0.244 TM |
| 0.121 TM | 0.318 NP | 0.366 M | 0.377 NP | 0.345 NP | 0.366 M | 0.234 M |
| 0.117 M | 0.258 M | 0.355 NP | 0.359 M | 0.290 TM | 0.240 TM | 0.164 NP |
| *Relative growth ($g \cdot g^{-1} \cdot d^{-1}$)·100* | | | | | | |
| 0.44 NP | 2.67 TM | 4.09 TM | 5.12 TM | 4.36 NP | 4.40 M | 2.97 M |
| 0.21 TM | 1.85 NP | 4.01 NP | 4.49 M | 4.28 M | 3.81 NP | 2.74 TM |
| 0.17 M | 1.39 M | 3.49 M | 3.94 NP | 2.92 TM | 2.68 TM | 1.29 NP |

muskellunge, and 21°C for the hybrid. The optimal temperatures of northern pike and muskellunge were within their respective ranges of temperatures where maximum growth occurred in experiments, and the optimal temperature for the hybrid fell between the two temperatures where greatest growth occurred in experiments. When the same simulations were run with $P$ reduced to 40%, optimal temperatures for growth decreased about 3°C for all taxa. This follows the idea that optimal temperature for growth decreases as ration decreases (Kitchell et al. 1977).

## Bioenergetics Model Simulations

Even though we determined ration levels with the bioenergetics model using target weights from actual esocid field studies, the simulations (given available inputs) might not accurately predict changes in biomass experienced in the field. However, these simulations can predict differences among the three fishes and the importance of thermal regime, ration levels, and stocking date relative to these differences. The results of these simulations are found in Fig. 5; those simulations labeled

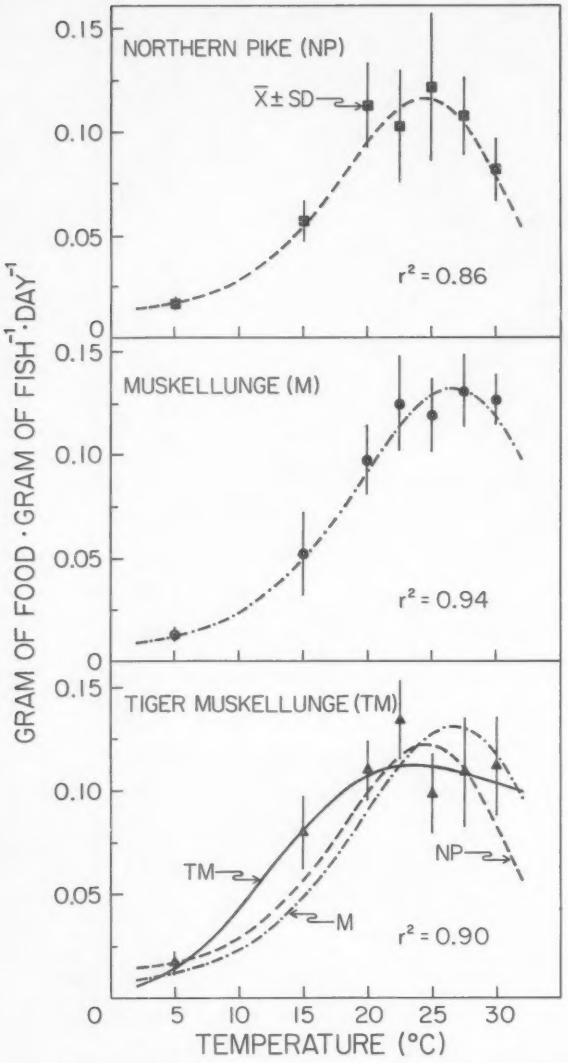


FIG. 3. Mean food consumption rates of northern pike, muskellunge, and tiger muskellunge determined in 2-wk laboratory experiments. Third-order polynomial curves were generated to fit these data; the bottom panel compares the curves of all three fishes.

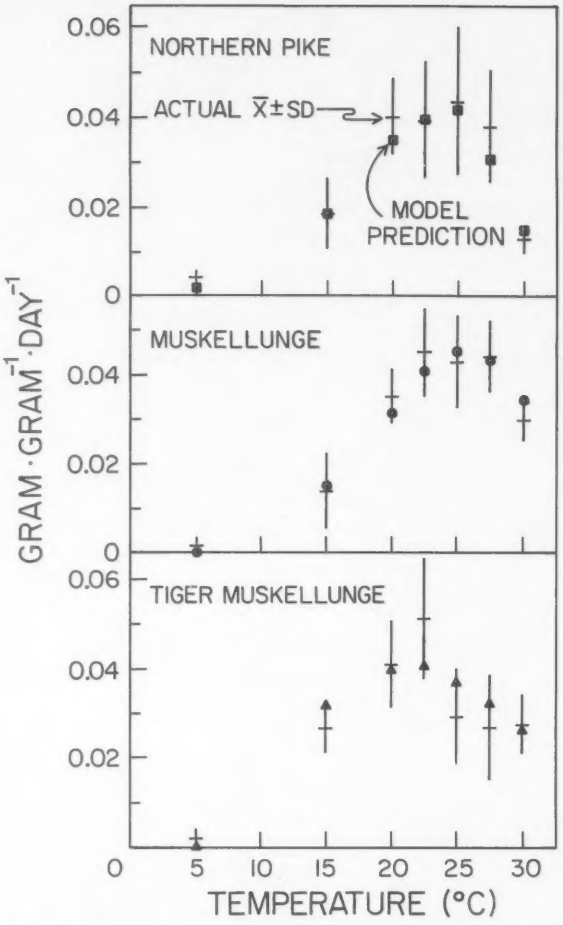


FIG. 4. Comparison of observed growth rates from 2-wk laboratory experiments and predicted growth rates (simulation of laboratory experiments) from a bioenergetics model for young-of-year esocids.

"C" differ from the "W" simulations only in that they were performed with the cool regime (C) instead of the more typical warm regime (W). Below, we examine two of these simulations in some detail.

*Simulation 1W*

In the warm thermal regime with constant ration, summer-stocked tiger muskellunge reached a greater final weight after 15 mo than either parent. Tiger muskellunge were 22 and 32% larger (by weight) than muskellunge and northern pike, respectively, and muskellunge were 9% larger than northern pike. (Note: percent weight differences were calculated as 100 × weight difference/weight of smaller fish.) These differences can be explained by examining the growth of these fishes throughout the simulation (Fig. 6, upper panel). During the first 3 mo following stocking (July, August, and September), warm temperatures (>20°C) allowed the muskellunge to grow fastest. As temperatures cooled from 20 to 10°C in October and November, muskellunge growth rates declined more rapidly than those of northern pike or tiger muskellunge, resulting in a weight advantage for the hybrid by the end of the first growing season. At this same time, cool temperatures allowed the northern pike weight to approach that of the muskellunge. Little or no growth occurred during winter. As temperatures warmed in spring, northern pike and hybrids began growing before muskellunge, and the hybrid increased its size advantage over its parents. However, warm temperatures in July and August temporarily slowed growth of northern pike and tiger muskellunge, resulting in a final ranking of sizes: tiger muskellunge > muskellunge > northern pike. The seasonal growth cycle that was produced by this simulation was typical of fish growth in temperate zones.

*Simulation 3W*

When the constant ration scheme (as in 1W) was replaced with a variable ration scheme in this simulation with the warm thermal regime and summer stocking, the final sizes of all taxa

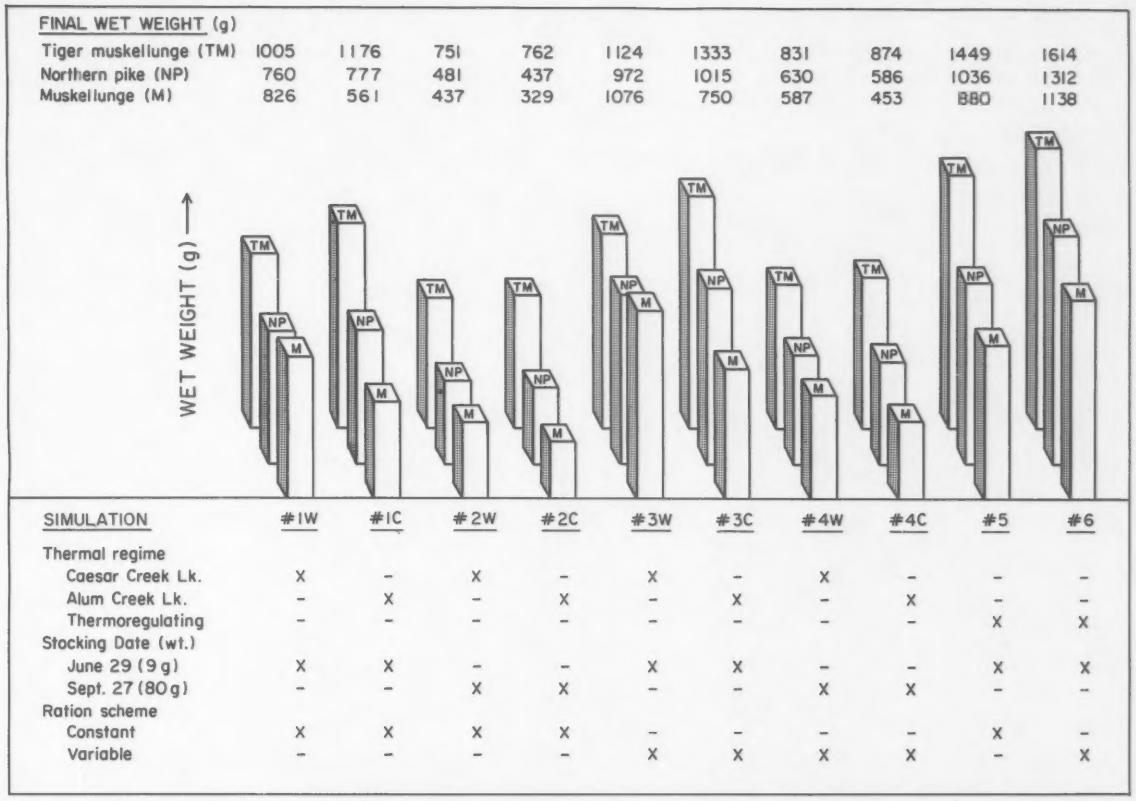
FINAL WET WEIGHT (g)
Tiger muskellunge (TM) 1005 1176 751 762 1124 1333 831 874 1449 1614
Northern pike (NP) 760 777 481 437 972 1015 630 586 1036 1312
Muskellunge (M) 826 561 437 329 1076 750 587 453 880 1138
WET WEIGHT (g)
TM
NP
M
SIMULATION #1W #1C #2W #2C #3W #3C #4W #4C #5 #6
Thermal regime
Caesar Creek Lk. X - X - X - X - - -
Alum Creek Lk. - X - X - X - X - -
Thermoregulating - - - - - - - - X X
Stocking Date (wt.)
June 29 (9 g) X X - - X X - - X X
Sept. 27 (80 g) - - X X - - X X - -
Ration scheme
Constant X X X X - - - - X -
Variable - - - - X X X X - X

FIG. 5. Different combinations of variable components (thermal regime (C = cool, W = warm), stocking date and weight, and ration) used in growth simulations of juvenile tiger muskellunge, northern pike, and muskellunge (lower panel), and the final weights (g) achieved with these simulations by September 27 of year following stocking (upper panel).

increased an average of 23%. Rank order of sizes remained the same, but relative differences between the hybrid and the smaller parent species decreased (tiger muskellunge and muskellunge weights were nearly the same, both about 14% greater than northern pike). The advantage that the hybrid had was reduced because the lowest ration (40% of $C_{max}$) occurred in spring when cool temperatures (10–20°C) most favored the hybrid.

Figure 6, lower panel, illustrates how the advantage in growth shifted from taxon to taxon depending on temperature and ration level. During the first 3 mo of the simulation (July–September), muskellunge grew faster because of the warmer temperatures. As temperatures declined in fall (October–November), the hybrid grew fast enough to surpass the parent species. Very little growth, if any, occurred during winter (December–February). When temperatures warmed in spring (March–May), the hybrid began growing soonest, but its growth was suppressed by low ration (40% of $C_{max}$). Growth rates increased noticeably when ration levels increased to 55% in June and July. Hot temperatures at the end of July caused a marked reduction in growth of northern pike and tiger muskellunge; at this point, muskellunge size surpassed that of northern pike and approached that of tiger muskellunge. High ration and high temperatures in late summer (August–September) allowed muskellunge to grow to nearly the size of tiger muskellunge and increase its small advantage over northern pike.

Under all conditions tested, tiger muskellunge grew fastest in every simulation. This supports claims of hybrid vigor even though it was not evident in the individual laboratory results. The hybrid growth advantage manifests itself due to combined effects of temperature and ration. In our simulations, thermal regimes alone favored tiger muskellunge because of prolonged periods of moderate temperatures (10–20°C) in spring and fall which were nearly optimal for their growth. Because more northerly lakes (extreme northern United States and Canada) have short warming and cooling periods (Diana 1982) and southern lakes have long periods during summer when temperatures are >25°C, thermal regimes of these systems might not favor the hybrid over its parents.

Northern pike grew faster than muskellunge except when summer stocking was coupled with the warm thermal regime. In this simulation, high temperatures during summer were less favorable to northern pike. These results, like those from laboratory experiments, support the hypothesis that northern pike should do better than muskellunge at cool temperatures and less well at warm temperatures.

Tiger muskellunge grew faster with the cool thermal regime than in corresponding simulations with the warm regime. Muskellunge always grew better in the warm system. Northern pike grew better in the cool system when stocked in summer, but better in the warm system when stocked in fall. Simulated thermoregulation increased growth in all three taxa. Mus-

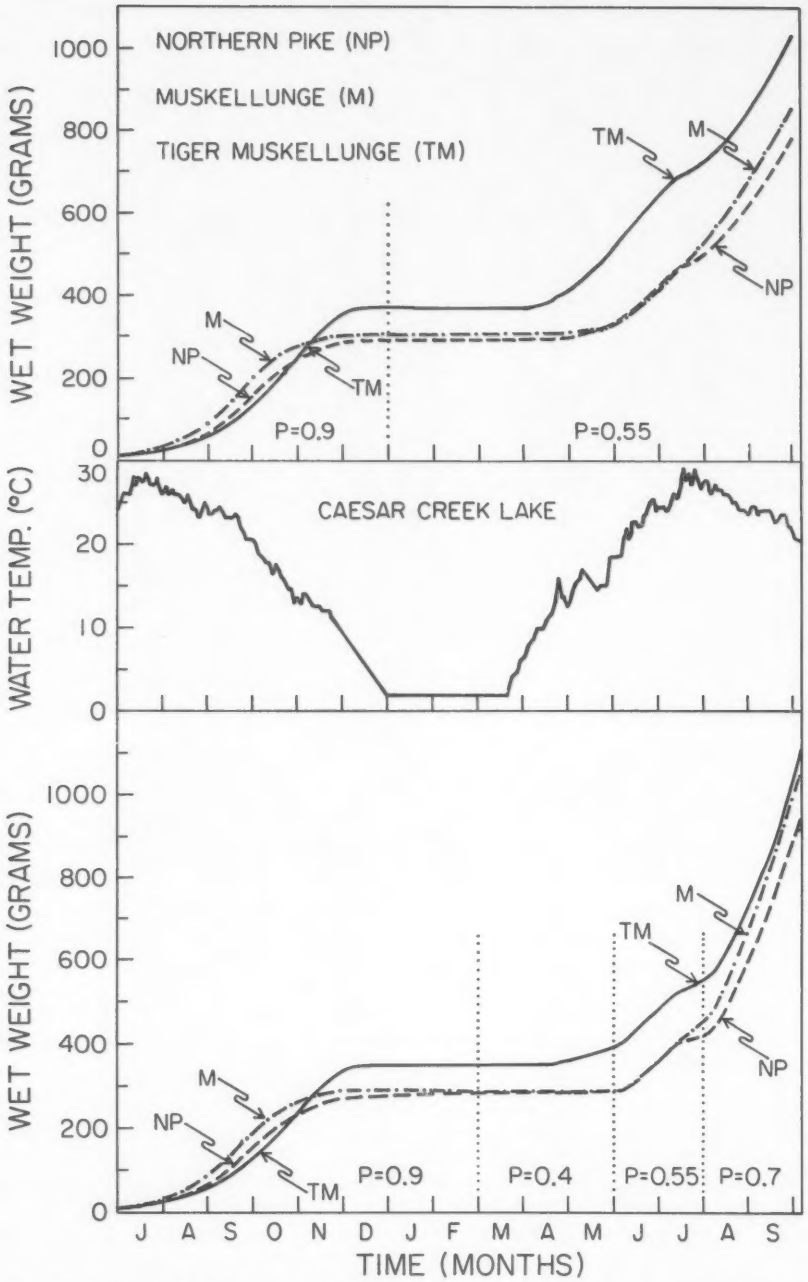


FIG. 6. Computer-simulated growth of summer-stocked esocids in a warm regime exposed to the constant ration scheme shown in the top panel (simulation 1W) and the variable ration scheme shown in the bottom panel (simulation 3W).

kellunge benefitted least from thermoregulation, because its thermoregulation temperatures differed least from lake temperatures. In systems with a shallow oxygenated epilimnion, where the benefits of thermoregulation would be limited, the advantage of tiger muskellunge would be reduced. As available epilimnetic temperatures increased, tiger muskellunge would be forced to spend time at temperatures farther from their optimal temperature (21°C) than either northern pike (24°C) or muskellunge (26°C).

With other conditions held constant (compare simulations 1 and 3 with 2 and 4, respectively), fish stocked in summer grew to a larger size than those stocked in fall, apparently because the

fish can grow faster in the field than in hatcheries during the 3 mo between summer and fall stocking dates. This could be due to a greater availability of forage and/or optimal temperatures in the field.

Best growth for all taxa was obtained when the prey base varied seasonally such that forage was most available during times when lake temperatures were most favorable for growth (compare simulations 1 and 2 with 3 and 4, respectively). However, as ration was varied seasonally, optimal temperatures sometimes did not coincide with high ration levels. For example, in May of simulation 3W (Fig. 6) when cool temperatures favored growth of tiger muskellunge, ration was only 40% of $C_{max}$; hence, tiger muskellunge grew slowly. In this same simulation, when hybrid growth was least favored by warm temperatures (August), ration was high, 70% of $C_{max}$. These conditions reduced differences in final sizes among the three taxa compared with differences when ration was constant (simulation 1W). In turn, if ration was overestimated in spring or underestimated in summer, hybrid advantage could possibly disappear.

## Discussion

Maximum growth of northern pike occurred at 25°C (24°C in simulations), which is 6° higher than the optimum temperature (19°C) that Casselman (1978) found within a Canadian stock of northern pike. Casselman also found that growth ceased at 28°C and that 29.4°C was the upper incipient lethal temperature. However, in our study, northern pike at 30°C were still growing. This suggests that local stocks might have adapted to the warm temperature regimes of Ohio waters during the 25 yr they have been maintained in Ohio hatchery ponds. Maximum growth and conversion efficiency of tiger muskellunge occurred at 22.5°C. Meade et al. (1983) found nearly the same results (maximum growth and efficiency at 23°C) for juvenile tiger muskellunge (120–130 mm) from parental stocks of a similar latitude (Pennsylvania) to Ohio. Our conversion efficiencies across the middle range of temperatures (15–25°C) for all three taxa ranged from 25 to 38%. These values compare favorably with those reported by Diana (1983) for YOY northern pike (42%; simulated), Johnson (1966) for YOY northern pike (30%; actual), Gammon (1963) for YOY muskellunge (37%; actual), and Brett and Groves (1979) for a typical young carnivorous fish (29%; averaged from actual data).

Since our study was completed, Diana (1983) also has published an energy budget for northern pike. Some notable differences exist between our study and his regarding the determination of parameters. Diana (1983) determined respiration rates for a larger size range of fish (5–1900 g versus 9–53 g), but at just two temperatures (compared with five in our work) and with a smaller sample size. The larger size range enabled Diana (1983) to develop a weight-dependent coefficient ($b_2$) which was also used in our study. Because Diana (1983) used only two temperatures, his temperature-dependent coefficient ($m = 0.16$) has a high potential for error; data at a third temperature might substantially modify his value for $m$. Diana's $m$ value translates to a $Q_{10}$ of 5.0. Brett and Groves (1979) suggested a general $Q_{10}$ of 2.3, and our $Q_{10}$ was 1.7. Though statistical comparisons of values from these two studies are difficult because of differences in fish sizes, the actual data points do not appear as different as do the values of $a^2$ (0.1025 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ (our study), 0.021 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ (Diana 1983)), and $m$ (0.055 (our study), 0.16 (Diana 1983)) in their respective respiration curves.

Dolinin (1973) investigated the respiration of a Russian population of northern pike across temperature. A comparison of the oxygen consumption (mg $O_2 \cdot g^{-1} \cdot h^{-1}$) for a 600-g (approximate mean size used by Dolinin) northern pike determined experimentally (Dolinin 1973) and by equation (our study and Diana 1983) follows:

| Temperature (°C) | Dolinin (1973) | Our study | Diana (1983) |
|---|---|---|---|
| 5 | 0.020 | 0.043 | 0.015 |
| 10 | 0.040 | 0.056 | 0.033 |
| 15 | 0.070 | 0.074 | 0.073 |
| 20 | 0.107 | 0.097 | 0.163 |
| 25 | — | 0.128 | 0.363 |

Dolinin's (1973) observed data lie intermediate between the two sets of predicted values. Because metabolic rates are so low at ≤5°C, these differences are probably not as important as those at ≥20°C. The differences among these studies might be due to something other than experimental differences; the different geographical locations and thermal history of separate populations of fish might cause the fish to react differently across a range of temperatures.

Diana (1983) also determined factors for excretion, egestion, and SDA. However, he was not able to obtain a balanced budget with these values, so we chose to use the general values presented in Brett and Groves (1979).

How important are the simulated size differences among the three esocids? Some evidence suggests that the esocid that grows fastest as a juvenile will not necessarily grow fastest as an adult (Hess 1981). This observation might cancel any advantage fast-growing juveniles might possess. However, size differences among taxa after both the first and second growing seasons (nearly 90% in weight in some simulations) should be large enough to influence survival. Large fish are less susceptible to natural mortality (Kipling and Frost 1970) and predation (Stein et al. 1981) and have wider diet range with respect to prey size than small fish (Gillen et al. 1981). Wide diet ranges might enhance survival during periods when preferred sizes of prey are scarce, as in winter or spring. These factors probably influence survival more strongly when fish are young; therefore, growth during the first year of life might be most critical to long-term survival.

However, growth and final size at the end of 12–15 mo are not the only considerations in generating appropriate stocking policy. Small esocids stocked in summer may be susceptible to intense predation by largemouth bass at stocking (Stein et al. 1981); only stocked hybrids greater than 250 mm (the large size in the simulations) are invulnerable to these predators. Consequently, managers must weigh the benefits of the eventual large size of summer-stocked fish against the higher short-term survival of fall-stocked fish. Clearly, if few summer-stocked fish survive, long-term growth differential becomes unimportant. Also, when stocking different sizes of fish during different seasons, the match between predator size and prey size becomes important. Small fishes with narrow diet ranges may be less likely to grow as well as their large counterparts, which are able to consume a wide range of prey (Gillen et al. 1981). Thus, the bioenergetics model should be used in conjunction with information on predator–prey size ratios, vulnerability to resident predators, and other factors not incorporated into this approach.

Another factor to weigh when considering various stocking strategies is the apparent adaptability of northern pike to the

warm waters encountered in Ohio reservoirs. This plasticity in northern pike which allows them to adapt to warm environments, given the necessary time to do so, could be an important consideration in continuing efforts to stock non-native fishes. If such plasticity is inherent in other fishes, it should be considered when deciding where to obtain fish for stocking, i.e. from a particular race or subspecies, or from a particular geographic region or latitude. For example, if a coolwater species is being stocked in a region where warm summer temperatures may affect survival, then brood stock should be selected from a population that is as southern as possible. Given the adaptability of these fish and their apparent difference from Canadian stocks, caution should be taken in extending the results of this study to populations of esocids outside the midwestern United States.

Bioenergetic models can aid management decision-making and suggest areas for further field research. In this case, the large differences in final weights between simulations with variable ration and those with constant ration suggest that accurate estimation of ration is necessary to estimate growth. The ration values we used were only rough estimates based on prey abundances. More accurate data on seasonal ration levels and their relationship to prey abundance and availability are needed, especially for young fish. Another important quality of the model is its flexibility. For example, given changes in mean weight through time, rate of food consumption can be determined; Cochran and Rice (1982) estimated largemouth bass food consumption over a 4-mo period using mean weights measured on nine sampling dates. If quantitative estimates of prey populations are coupled with this analysis, correlations of prey availability with actual consumption could be formulated, thereby enabling one to predict consumption rates based on prey availability data and vice versa. If initial population size and mortality rates are included in the model, the quantity of forage necessary to support a population or to achieve a desirable size of predator can be determined (Stewart et al. 1981). In this form the model also can predict the predatory effect on a prey population. With historical knowledge of year-to-year fluctuations in the prey base, a maximum level of predation can be defined based on minimum population levels of the prey, thus providing useful information for determining maximum stocking densities of predators.

The model could also be applied to estimate the uptake and accumulation of pollutants (e.g. heavy metals, radioisotopes, and pesticides). This type of modelling has already been done with northern pike (Carlsson 1978; Fagerstrom and Asell 1973; Fagerstrom et al. 1974), but these models were developed with little actual northern pike data. The temperature-related and weight-related data presented here and in Diana (1983) should be very useful for this type of modelling in the future.

In summary, the experimental data suggest that the physiological differences between the parent species with regard to temperature are related to the latitudinal differences in their natural geographic distributions, and that the hybrid is not particularly similar to either parent. The Ohio stock of northern pike, whose brood stock is maintained in hatchery ponds, has apparently adapted to warm Ohio waters. If this apparent adaptation had not occurred, a larger difference between the northern pike and muskellunge might be expected. Based on bioenergetic considerations, tiger muskellunge outgrew both northern pike and muskellunge in a thermal regime common to Ohio waters and in a cooler thermal regime, which was atypical of Ohio systems. In systems with few predators and an abundant prey base of soft-rayed fishes, this hybrid should outgrow and perhaps survive better than its parents. Comparative work that better defines the role of resident predators and forage base on the survival and growth of all three taxa is required before definitive taxon-specific stocking recommendations can be made.

## Acknowledgements

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## References

BEAMISH, F. W. H. 1970. Oxygen consumption of largemouth bass, *Micropterus salmoides*, in relation to swimming speed and temperature. Can. J. Zool. 48: 1221–1228.

BEAMISH, F. W. H., AND L. M. DICKIE. 1967. Metabolism and biological production in fish, p. 215–242. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, England. 495 p.

BEAUCHAMP, J. J., AND J. S. OLSON. 1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54: 1403–1407.

BEVELHIMER, M. S. 1983. Assessing significance of physiological differences among three esocids with a bioenergetics model. Masters thesis, The Ohio State University, Columbus, OH. 49 p.

BONIN, J. D., AND J. R. SPOTILLA. 1978. Temperature tolerance of larval muskellunge (*Esox masquinongy* Mitchill) and $F_1$ hybrids reared under hatchery conditions. Comp. Biochem. Physiol. 59A: 245–248.

BRETT, J. R. 1962. Some considerations in the study of respiratory metabolism in fish, particularly salmon. J. Fish. Res. Board Can. 19: 1025–1038.

1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 22: 1491–1501.

BRETT, J. R., AND T. D. D. GROVES. 1979. Physiological energetics, p. 279–352. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. 8. Academic Press, New York, NY. 786 p.

CARLSSON, S. 1978. A model for the turnover of 137 Cs and potassium in pike (*Esox lucius*). Health Phys. 35: 549–554.

CASSELMAN, J. M. 1978. Effects of environmental factors on growth, survival, activity, and exploitation of northern pike. Am. Fish. Soc. Spec. Publ. 11: 114–128.

COCHRAN, P. A., AND J. A. RICE. 1982. A comparison of bioenergetics and direct field estimates of cumulative seasonal food consumption by largemouth bass (*Micropterus salmoides*), p. 88–96. *In* G. M. Caillet and C. A. Simenstad [ed.] GUTSHOP '81: Fish food habits studies, proceedings of the third Pacific workshop. Washington Sea Grant, Seattle, WA.

CROSSMAN, E. J. 1978. Taxonomy and distribution of North American esocids. Am. Fish. Soc. Spec. Publ. 11: 13–26.

DIANA, J. S. 1980. Diel activity patterns and swimming speeds of northern pike (*Esox lucius*) in Lac Ste. Anne, Alberta. Can. J. Fish. Aquat. Sci. 37: 1454–1458.

1982. An experimental analysis of the metabolic rate and food utilization of northern pike. Comp. Biochem. Physiol. 71A: 395–399.

1983. An energy budget for northern pike (*Esox lucius*). Can. J. Zool. 61: 1968–1975.

DIANA, J. S., AND W. C. MACKAY. 1979. Timing and magnitude of energy deposition and loss in the body, liver, and gonads of northern pike (*Esox lucius*). J. Fish. Res. Board Can. 36: 481–487.

DOLININ, V. A. 1973. The rate of basil metabolism in fish. J. Ichthyol. 13: 430–438.

ELLIOTT, J. M. 1976. Energy losses in the waste products of brown trout (*Salmo trutta* L.). J. Anim. Ecol. 45: 561–580.

ELLIOTT, J. M., AND W. DAVIDSON. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19: 195–201.

FAGERSTROM, T., AND B. ASELL. 1973. Methyl mercury accumulation in an aquatic food chain. Ambio 2: 164–171.

FAGERSTROM, T., B. ASELL, AND A. JERNELOV. 1974. Model for accumulation of methyl mercury in northern pike *Esox lucius*. Oikos 25: 14–20.

GAMMON, J. R. 1963. Conversion of food in young muskellunge. Trans. Am. Fish. Soc. 92: 183–184.

GILLEN, A. L., R. A. STEIN, AND R. F. CARLINE. 1981. Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. Trans. Am. Fish. Soc. 110: 197–209.

HEADRICK, M. R., M. S. BEVELHIMER, R. F. CARLINE, AND R. A. STEIN. 1982. Evaluation of fish management techniques: evaluation of stocking northern pike in Ohio lakes. Ohio Federal Aid Project F-57-R. Ohio Division of Wildlife, Columbus, OH.

HELWIG, J. T., AND K. A. COUNCIL. 1979. SAS user's guide, 1979 edition, SAS Institute Inc., Cary, NC. 494 p.

HESS, L. J. 1981. Evaluations of esocid stockings in West Virginia. Division of Wildlife Resources. Federal Aid Project F-53-R. Department of Natural Resources, Charleston, WV.

HESSER, R. B. 1978. Management implications of hybrid esocids in Pennsylvania. Am. Fish. Soc. Spec. Publ. 11: 302–307.

JENKINS, K. M. 1979. Predator–prey relations in reservoirs, p. 123–134. *In* R. Stroud and H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, DC. 504 p.

JOBLING, M. 1981. The influences of feeding on the metabolic rates of fishes: a short review. J. Fish Biol. 18: 385–400.

JOHNSON, L. 1966. Experimental determination of food consumption of pike, *Esox lucius*, for growth and maintenance. J. Fish. Res. Board Can. 23: 1495–1505.

KIPLING, C., AND W. E. FROST. 1970. A study of the mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. J. Anim. Ecol. 39: 115–157.

KITCHELL, J. F., AND J. E. BRECK. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2159–2168.

KITCHELL, J. F., D. J. STEWART, AND D. WEININGER. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1922–1935.

MEADE, J. W., W. F. KRISE, AND T. ORT. 1983. Effect of temperature on production of tiger muskellunge in intensive culture. Aquaculture 32: 157–164.

MOODY, R. C., J. M. HELLAND, AND R. A. STEIN. 1983. Escape tactics used by bluegills and fathead minnows to avoid predation by tiger muskellunge. Environ. Biol. Fishes 8: 61–65.

PECOR, C. H. 1978. Intensive culture of tiger muskellunge in Michigan during 1976 and 1977. Am. Fish. Soc. Spec. Publ. 11: 202–209.

PIERCE, R. G., T. E. WISSING, J. G. JAWORSKI, AND R. N. GIVENS. 1980. Energy storage and utilization patterns of gizzard shad in Acton Lake, Ohio. Trans. Am. Fish. Soc. 109: 611–616.

RICE, J. A., J. E. BRECK, S. M. BARTELL, AND J. F. KITCHELL. 1983. Evaluating the constraints of temperature, activity, and consumption on growth of largemouth bass. Environ. Biol. Fishes 9: 263–275.

SCOTT, D. P. 1964. Thermal resistance of pike (*Esox lucius* L.), muskellunge (*E. masquinongy* Mitchill), and their $F_1$ hybrid. J. Fish. Res. Board Can. 21: 1043–1049.

STEIN, R. A., R. F. CARLINE, AND R. S. HAYWARD. 1981. Largemouth bass predation on stocked tiger muskellunge. Trans. Am. Fish. Soc. 110: 604–612.

1982. Evaluation of fish management techniques: evaluation of stocking tiger muskies into Ohio lakes. Ohio Federal Aid Project F-57-R. Ohio Division of Wildlife, Columbus, OH.

STEWART, D. J., J. F. KITCHELL, AND L. B. CROWDER. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110: 751–763.

TRAUTMAN, M. B. 1957. The fishes of Ohio. The Ohio State University Press, Columbus, OH. 683 p.

WEBB, P. W. 1977. Fast-start performance and body form in seven species of teleost fish. J. Exp. Biol. 74: 211–226.

WEBSTER, J., A. TRANDAHL, AND J. LEONARD. 1978. Historical perspective of propagation and management of coolwater fishes in the United States. Am. Fish. Soc. Spec. Publ. 11: 161–166.

WEITHMAN, A. S., AND R. O. ANDERSON. 1977. Survival, growth, and prey of esocidae in experimental systems. Trans. Am. Fish. Soc. 106: 424–430.

WOHLSCHLAG, D. E., AND R. O. JULIANO. 1959. Seasonal changes in bluegill metabolism. Limnol. Oceanogr. 4: 195–209.

# Dissipation of Permethrin in Limnocorrals

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Solomon, K. R., J. Y. Yoo, D. Lean, N. K. Kaushik, K. E. Day, and G. L. Stephenson. 1985. Dissipation of permethrin in limnocorrals. Can. J. Fish. Aquat. Sci. 42: 70–76.

Permethrin (3-phenoxybenzyl(1RS)-*cis*,*trans*-3-(2,2-dimethyl-3-dichlorovinyl)-2,2-dimethylcyclopropanecarboxylate) applied to approximately 100-$m^3$ enclosures (limnocorrals) in a small mesotrophic lake in Southern Ontario (47°51′25″N; 77°25′30″W) at concentrations of 500, 50, 5, and 0.5 $\mu g \cdot L^{-1}$ dissipated from the water rapidly and approximated first-order kinetics in the first 8–12 d. Time taken for 50 and 90 % dissipation ranged from 1.65 and 3.65 d, respectively, at 0.5 $\mu g \cdot L^{-1}$ to 3.5 and 6.75 d, respectively, at 50 $\mu g \cdot L^{-1}$. Inter- and intra-seasonal replication of dissipation patterns was good. Rate of dissipation varied slightly with depth, normally being slower at greater depth. Absorption of permethrin to sediments was rapid, penetration shallow, and disappearance slow. Permethrin had no effect on water chemistry but there was an increase in the Secchi disk depth in the treated limnocorrals. Dissolved inorganic carbon decreased in all limnocorrals, including controls after treatment, suggesting precipitation of calcium carbonate which may act as a scavenging agent for permethrin in the water. Limnocorrals are a useful tool for evaluating the behavior of pesticides in the aquatic system.

Nous avons appliqué 500, 50, 5 et 0,5 $\mu g \cdot L^{-1}$ de perméthrine (cyclopropanecarboxylate de 3-phénoxybenzyl(1RS)-*cis*,*trans*-3-(2,2-diméthyl-3-dichlorovinyl)-2,2-diméthyle) dans des secteurs d'environ 100 $m^3$ du limnocorail d'un petit lac mésotrophe situé dans le sud de l'Ontario (47°51′25″N ; 77°27′30″O) ; le produit s'est rapidement dissipé, atteignant une vitesse de premier ordre 8 à 12 jours après l'application. Il s'était dissipé 50 et 90 % du produit au bout de 1,65 jour et de 3,65 jours respectivement à 0,5 $\mu g \cdot L^{-1}$, et au bout de 3,5 jours et 6,75 jours respectivement à 50 $\mu g \cdot L^{-1}$. Le mode de dissipation s'est reproduit dans une mesure satisfaisante durant une même saison et d'une saison à l'autre. La vitesse de dissipation variait légèrement selon la profondeur ; la dissipation était normalement plus lente en eau profonde. La perméthrine a été rapidement absorbée dans les sédiments, elle n'a pas pénétré profondément et elle est disparue lentement. Elle n'a eu aucun effet sur les propriétés chimiques de l'eau, mais le disque de Secchi atteignait une plus grande profondeur dans les zones de limnocorail traitées. La teneur des eaux en carbone inorganique dissous a diminué dans tous les secteurs, y compris les secteurs témoins, après le traitement, ce qui indiquerait qu'il y a eu formation d'un précipité de carbonate de calcium, composé qui pourrait capter la perméthrine de l'eau. L'étude des limnocoraux est un moyen utile de voir ce qu'il advient des pesticides en milieu aquatique.

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The increased use of pesticides in both agricultural and urban areas has resulted in widespread concern that these chemicals may adversely affect nontarget areas such as aquatic ecosystems. The ecological effects of a pesticide in any system are dependent on the inherent toxicity as well as the bioavailability of the compound, and a number of methods have been used to assay these parameters. Acute and chronic laboratory toxicity studies on single organisms have been extensively used; however, the conditions under which these are conducted are often unrealistic and the extrapolation of the results to field conditions are not necessarily valid. Thus, model ecosystems have been developed. These range from small-volume aquaria and continuous culture systems (Metcalf et al. 1971; Draggan 1976a, 1976b; Taub 1976) to complex large-volume marine, lake, and stream simulators (Beers et al. 1977; Blinn et al. 1977; Davies and Gamble 1979; Kuiper 1977, 1981; Menzel and Case 1977; Lack and Lund 1974; Leah et al. 1978; Twinch and Breen 1981; Marshall and Mellinger 1980).

However, model systems have not necessarily been realistic in terms of climatic conditions or species composition, and the larger complex systems lack replication and have not been used for pesticide studies. The application of pesticides to natural ponds, pools, or lakes does provide realistic data on the impact of a pesticide (Anderson 1970; Ali and Mulla 1978; Stephenson 1982; Crossland 1982; Crossland et al. 1982). Unfortunately, such studies are difficult to replicate. Artificial ponds, either

constructed of concrete or plastic materials, can be replicated but may not have communities similar to those found in natural systems (Hurlbert et al. 1972; Hughes et al. 1980; Rawn et al. 1982). Furthermore, sediments form over long periods of time and the community and biogeochemical processes related to sediments may be poorly represented in artificial pond and microcosm studies.

An obvious need for replicate and more realistic methods to evaluate the effects of pesticides in the aquatic ecosystem has led us to investigate the use of enclosures or limnocorrals by which a natural body of water may be divided into a number of separate compartments for experimental purposes (Solomon et al. 1980). The approach has been used to study other aquatic pollutants, and Shires (1983) has used 1-$m^3$ stainless steel containers to determine the impact of cypermethrin in fish and zooplankton in freshwater ponds. This, and a companion paper (Kaushik et al. 1985), describe the application of the insecticide permethrin to these enclosures, both in terms of the persistence and biological impact of the pesticide. The objectives of this study were twofold: to develop a methodology for studying the effects of pesticides in enclosures and to determine the impact of permethrin on the aquatic ecosystem.

## Materials and Methods

The limnocorrals were set up in Lake St. George, a 10-ha mesotrophic lake situated near King City, Ont. (47°51′25″N; 77°25′30″W). The enclosures, manufactured by Fell-Fab of Burlington, Ont., were constructed from a flexible, nylon-reinforced polyvinyl chloride plastic, were 5 × 5 × 5 m deep, supported at the surface by a 15-cm diameter expanded polyethylene flotation collar and weighted at the base with 20 m of 6-mm steel chain. The limnocorrals were attached to wooden frames, installed in 4–4.5 m of water as described before (Solomon et al. 1980), and depending on depth, enclosed a volume of 98–120 $m^3$ of lake water open to the air at the surface and enclosing the sediments to a depth of approximately 15 cm at the bottom. Prior to use, the seal between the base of the limnocorral and the sediments was confirmed by SCUBA inspection. Ten limnocorrals were used in the summer of 1979 and 9 in 1980.

The increasing use of permethrin (3-phenoxybenzyl (1RS)-*cis*,*trans*-3-(2,2-dimethyl-3-dichlorovinyl)-2,2-dimethylcyclopropanecarboxylate) and the other synthetic pyrethroids in food and fiber production led us to choose it as a model compound. Because of uncertainty in the rate of mixing of permethrin in the water column (Boyce 1974), the pesticide was force-mixed with the water in the limnocorrals by use of an injection system developed in laboratory and field trials (Solomon et al. 1980) and powered by a 75-mm pump operating at 108 $m^3 \cdot h^{-1}$. While this method of mixing is unrealistic in terms of accidental or other overspray, it is probably a realistic model for entry of contaminated water from streams, etc., and does avoid uncertainty in the rates of vertical mixing in replicate corrals. This method also avoided the formation of high concentration gradients which may have had differential effects on organisms tending to congregate in the upper or lower regions of the corrals. The permethrin (86.6% technical, 40:60 *cis*:*trans*) was dissolved in 0.5 L of acetone and drawn into the suction hose of the pump over a period of 30 min. The pump was run for a further 30 min to ensure complete mixing. Three limnocorrals each were treated to give nominal concentrations of 50 and 5 $\mu g \cdot L^{-1}$ in the summer of 1979 and 5 and 0.5 $\mu g \cdot L^{-1}$ in the summer of 1980. Three limnocorrals were treated with 0.5 L of acetone in both years as controls. In addition to these concentrations, one limnocorral was treated with 500 $\mu g \cdot L^{-1}$ in the summer of 1979. The latter high concentration was used to test the mixing and residue analysis procedure and was completely unrealistic in terms of that which might normally be expected in an aquatic environment through agricultural or forest use of permethrin. The lower concentrations were in the same ranges as those reported for drift contamination by cypermethrin (0.4–1.7 $\mu g \cdot L^{-1}$, Crossland et al. 1982) under agricultural use conditions and for permethrin (0.26 $\mu g \cdot L^{-1}$) based on a surface application rate of 13.6 $g \cdot ha^{-1}$ (Kingsbury 1976).

Water samples for residue analysis were taken at regular intervals in 4-L glass bottles which were clamped in a weighted wire basket, lowered to the appropriate depth in each limnocorral, and allowed to fill. In the first season, the limnocorrals were sampled at 1, 2, and 3 m depths. Since differences in concentration with depth were small, integrated samples from the surface to 3.5 m depth were collected in 1980. Samples were transported to the laboratory, stored at 4°C, and extracted within 48 h. Analyses of preliminary samples taken from the 500-$\mu g$ corral showed that degradative loss and adsorption to the interior surface of the glass sample bottle during this period was less than 5%. While adsorption to containers is a potential problem in the sampling of pesticide solutions (Sharom and Solomon 1981a), it was not apparent in this study, possibly as a result of adsorption of permethrin to particulate matter in the water.

Physical and chemical characteristics of the lake water and enclosed water columns were also monitored at weekly to biweekly intervals in 1979 and at weekly or shorter intervals in 1980. Temperature and dissolved oxygen were measured between the hours of 10:00 and 16:00 at 0.5-m intervals up to 4.0 m depth with a YSI model 51A dissolved oxygen meter. A portable Accumet pH meter (model 150) was used to measure pH. Three integrated water samples (from surface to 3.5 m depth) were collected with a 25-mm-OD tube sampler (Solomon et al. 1982), pooled, and prepared for analysis at the Canada Centre for Inland Waters for nitrate, nitrite, ammonia, and dissolved organic and inorganic carbon using standard methods (Environment Canada 1979).

Adsorption of pesticide to sediment was measured by installing, by SCUBA diver prior to treatment, a number of 9-cm-ID × 10-cm-high plastic cups, filled with sediment on the bottom of the limnocorral. Nylon cords were attached to the cups for easy removal, and when samples were taken, a cover was lowered on the cord and the cup gently raised to the surface where cup and contents were frozen and held at −17°C. They were cut into an upper 2.5-cm section and a lower section with a band-saw. The sections of cup were discarded and the frozen sediment was freeze-dried and stored at −17°C until extraction. This technique was found to avoid detectable loss of permethrin in storage.

Permethrin residues in lake water were extracted from a 1.5-L aliquot of unfiltered water in a separatory funnel with 3 × 100 mL of pesticide grade hexane. The extract was dried with anhydrous sodium sulphate and the volume reduced to approximately 2 mL on a rotary evaporator. Permethrin residues in lake sediment were recovered by rehydrating a 5-g aliquot of the dried sediment with 25 mL of water, allowing this to stand for 16 h at 4°C, and then extracting with 150 mL of 20% acetone in hexane in a Soxhelet extractor for 6 h. This extract was washed with 3 × 100 mL of water, dried through 20 g of anhydrous

sodium sulphate, and the volume reduced to approximately 10 mL on a rotary evaporator.

A Bio-Sil A column (10 mm ID, 3 g Bio-Sil A, Bio Rad Laboratories) was used for clean-up of the extracts. The column was prepared in hexane, washed with a further 10 mL of hexane, run almost to dryness, and a 1- to 2-mL aliquot of the extract loaded onto the column. The column was washed with 3 × 1 mL of hexane and then eluted with 2.5% diethyl ether in hexane (v/v) at 1–2 mL·min$^{-1}$ and the permethrin collected in the 6- to 25-mL fraction. The residue was concentrated by evaporation of the solvent in a stream of nitrogen in a water bath at 45°C.

Permethrin concentrations were determined using a Tracor model 550 gas chromatograph equipped with a $^{63}$Ni electron capture detector. The 1 m × 4 mm ID glass column was packed with 3% (m/m) OV-101 on 100- to 120-mesh Gas Chrom Q. At a column temperature of 260°C, a detector temperature of 300°C, and a nitrogen carrier gas flow rate of 80 mL·min$^{-1}$, the retention time for permethrin was 2 min. *Cis* and *trans* isomers were not separated and total permethrin concentration was calculated from the peak height.

The analytical procedures were checked by fortification of distilled water, lake water, and sediments with analytical standards of permethrin (Table 1). The detection limit for permethrin in water was 30 ng·L$^{-1}$ and no permethrin was found in the control corrals or the lake itself either before or after treatment.

TABLE 1. Recovery of permethrin from fortified water and sediment samples (mean ± SD calculated from at least 10 replicates).

| Fortification rate | Sample | Mean recovery |
|---|---|---|
| 0.5 μg·L$^{-1}$ | Distilled | 94.5±1.8 |
| 5.0 | water | 99.5±1.5 |
| 50.0 | | 98.9±1.2 |
| 0.5 | Lake water | 96.0±2.8 |
| 5.0 | | 99.4±1.2 |
| 50.0 | | 103.7±3.5 |
| 0.2 mg·kg$^{-1}$ | Sediment | 101.9±5.4 |
| 2.0 | | 105.1±7.4 |

## Results and Discussion

Nitrate, nitrite, and ammonia concentrations (Table 2) were almost always near the detection limit and no differences in these and several other parameters were seen between control and treated corrals, suggesting that permethrin had little effect on lake water. Temperatures in the corrals were within 1° of those outside the corrals except immediately after mixing when temperatures were the same from top to bottom. Surprisingly, both oxygen and dissolved inorganic carbon concentrations decreased during the 55 d following treatment (Fig. 1). One would expect oxygen to mirror dissolved inorganic carbon (on a molar basis) depending on the balance between respiration and photosynthesis. To explain these results it should be recalled that dissolved inorganic carbon includes carbon dioxide, carbonate, and bicarbonate. Increasing temperature and/or pH would result in calcium carbonate precipitation. Within this 55-d period almost half the dissolved inorganic carbon was lost from the water even though dissolved inorganic carbon would have been produced as oxygen was consumed. If all the oxygen were used in respiration and neglecting input from the atmosphere, the additional loss of dissolved inorganic carbon would be 10% more than observed. For some of the period of observation the oxygen concentration in the water (Fig. 1) was below saturation and any invasion of atmospheric oxygen would further increase the loss of dissolved inorganic carbon. The formation and precipitation of calcium carbonate may be a significant scavenging agent for permethrin as well as other substances. In similar studies on cypermethrin in 1-m$^3$ metal enclosures, Shires (1983) observed no differences in dissolved oxygen, pH, conductivity, temperature, suspended solids, or chlorophyll *a* between control or treated enclosures or between concentrations in the treated enclosures.

Water in the treated corrals was clearer than the controls from about 25 to 50 d after treatment (Fig. 1). This may have resulted from increased or more efficient grazing by rotifers in the treated corrals (Kaushik et al. 1985) or from inhibition of phytoplankton growth by permethrin such as has been reported (Stratton and Corke 1981). Similar changes in clarity were not noted in small enclosures treated with cypermethrin (Shires 1983).

The dissipation rate of permethrin applied at 5 μg·L$^{-1}$ was rapid and the concentration fell to less than 0.1 μg·L$^{-1}$ by the end of 12 d (Fig. 2). The concentrations at 1, 2, and 3 m depth in corral 2 were 4.2, 4.5, and 4.3 μg·L$^{-1}$, respectively, immediately after treatment, confirming high mixing efficiency of the injection system. Average initial concentrations in the three

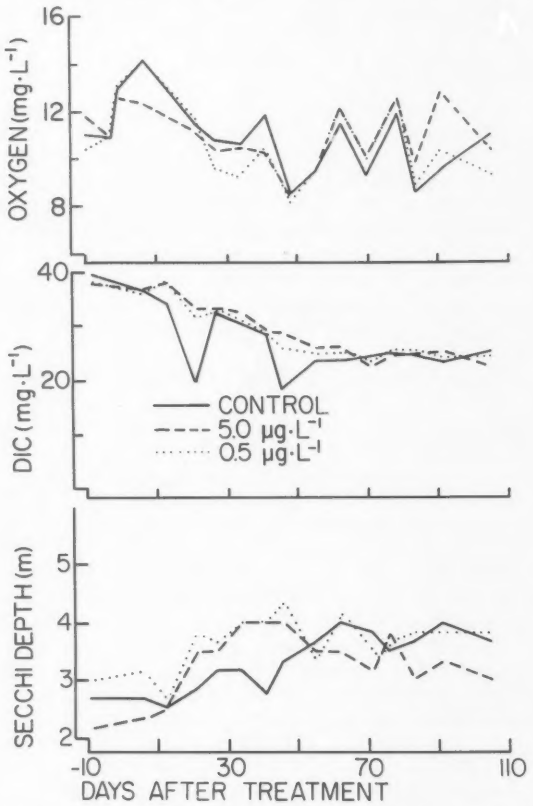


FIG. 1. Oxygen concentration (at 0.5 m), dissolved organic carbon (0–3.5 m depth), and Secchi disk readings in control corrals and corrals treated with nominal permethrin concentrations of 0.5 and 5 μg·L$^{-1}$ in 1980.

TABLE 2. Physical and chemical properties of the water in control and exposed limnocorrals in Lake St. George, 1979 and 1980.

| Observation | Mean (range) | | | |
|---|---|---|---|---|
| | June 26 – Oct. 2, 1979 | June 12 – Sept. 23, 1980 | | |
| | All corrals | Control | 5 $\mu g \cdot L^{-1}$ | 0.5 $\mu g \cdot L^{-1}$ |
| pH | 8.23(7.80–8.58) | 7.84(7.23–8.53) | 8.05(7.46–8.48) | 8.04(7.15–8.5) |
| Alkalinity (mg $CaCO_3 \cdot L^{-1}$) | 145(119–173) | — | — | — |
| Hardness (mg $CaCO_3 \cdot L^{-1}$) | 64(46–82) | — | — | — |
| Secchi disk (m) | 2.5(1.1–3.8) | 3.34 | 3.37 | 3.70 |
| Conductivity ($mS \cdot m^{-1}$) | 32.4(26.2–33.0) | 32.0(26.7–38.8) | 31.8(25–40) | 32.0(24.2–41.6) |
| Total Kjeldahl nitrogen ($mg \cdot L^{-1}$) | 0.94(0.77–1.54) | 0.60(0.48–0.71) | 0.57(0.49–0.70) | 0.66(0.51–0.97) |
| Temperature range at 1 m (°C) | 12–26 | 14–25 | 14–25 | 14–25 |
| Temperature range at 2 m (°C) | 12–25 | 14–25 | 14–25 | 14–25 |
| Temperature range at 3 m (°C) | 12–21 | 14–24 | 14–23 | 14–24 |
| Temperature range at 4 m (°C) | 12–14 | 9.3–19 | 13.3–19 | 13.2–19 |
| $NO_2$ ($\mu g \cdot L^{-1}$) | — | 2.07(1–5) | 2.14(1–4) | 2.0(1–6) |
| $NO_2NO_3$ ($\mu g \cdot L^{-1}$) | — | 13(3–60) | 13(5–77) | 11(5–60) |
| $NH_3$ ($\mu g \cdot L^{-1}$) | — | 5.6(1–15) | 5(1–16) | 5(1–22) |
| DOC ($mg \cdot L^{-1}$) | — | 8.65(5.4–12) | 8.72(5.8–12.2) | 8.66(2.4–10.7) |
| $O_2$ at 4.0 m ($mg \cdot L^{-1}$) | — | 4.88(0.09–12.1) | 5.12(0.34–13) | 6.57(0.07–13) |

replicate corrals were 0.87, 1.4, and 4.4 $\mu g \cdot L^{-1}$ in the order in which they were treated. The reason for this is thought to be adsorption to the plastic intake and discharge hoses on the pump, and the phenomenon was not observed at the higher concentration or in 1980, possibly due to saturation of available adsorption sites. In general, permethrin concentration did not vary with depth, either just after treatment or for the duration of the experiment, suggesting that if temperature and light penetration, which did vary with depth, had an influence on the dissipation of permethrin, this was balanced by vertical flux rates.

Treatment of corrals with 50 $\mu g \cdot L^{-1}$ (Fig. 2) gave results similar to those above except that there seemed to be a more consistent difference in the concentration of permethrin at each depth sampled. Here, the highest concentration was always at the greatest depth, suggesting some phenomenon resulting in less dissipation at greater depth. The results from the 5 $\mu g \cdot L^{-1}$ limnocorrals suggest that this is not a temperature or photolytic phenomenon. The concentration of permethrin is, however, close to that reported for the maximum water solubility (<0.1 $mg \cdot L^{-1}$; BCPC 1979), and the concentration gradient observed may be a consequence of precipitation of insoluble permethrin at a slow rate and a resulting accumulation of higher concentration at greater depth. Essentially similar results were obtained at 500 $\mu g \cdot L^{-1}$ (Fig. 2) although the rate of dissipation was not as rapid as one would expect taking into account the water insolubility of permethrin and the possibility of precipitation.

While it is probable that some of the permethrin in the water column was in solution, permethrin has a high affinity for particulate matter and sediments from Lake St. George (Sharom and Solomon 1981b), and most of the permethrin in the water column was likely adsorbed to particulate matter. Laboratory experiments to determine the ratio of adsorbed and dissolved permethrin were unsuccessful because of the tendency of permethrin to adsorb strongly to the filter paper, glass fiber filters, and Millipore filters (both cellulose acetate and polycarbonate) used to separate permethrin adsorbed to particulate matter from the solution.

During the summer of 1980, permethrin was again applied at rates of 5.0 as well as 0.5 $\mu g \cdot L^{-1}$ to three limnocorrals each. Because of time constraints and the previous observation that differences in concentration at different depths were small, integrated samples were taken to a depth of 3 m. Even though treatment was made 60 d earlier than in 1979, results in the limnocorrals treated at a rate of 5.0 $\mu g \cdot L^{-1}$ were similar to those seen in 1979 with initial concentrations in the three

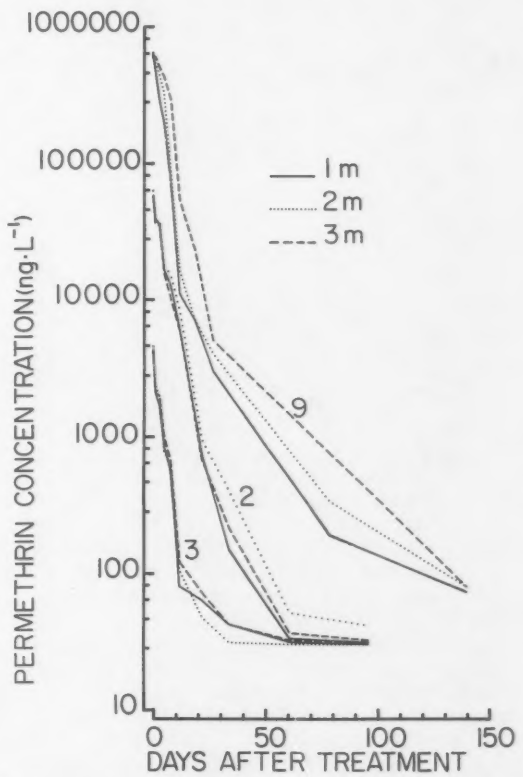


FIG. 2. Concentration of permethrin at 1, 2, and 3 m depths in corral 3 treated at a nominal concentration of 5 $\mu g \cdot L^{-1}$, corral 2 treated with a nominal concentration of 50 $\mu g \cdot L^{-1}$, and corral 9 treated with a nominal concentration of 500 $\mu g \cdot L^{-1}$ in 1979.

TABLE 3. Mean permethrin concentration in treated limnocorrals expressed as a percentage of initial concentration (mean and SE calculated from three replicate corrals; because initial concentrations varied from one limnocorral to the next, values were analyzed on the basis of percent of initial concentration).

| | 1980 | | | | 1979 | | | |
|---|---|---|---|---|---|---|---|---|
| | 0.5 $\mu g \cdot L^{-1}$ | | 5.0 $\mu g \cdot L^{-1}$ | | 5.0 $\mu g \cdot L^{-1}$ | | 50 $\mu g \cdot L^{-1}$ | |
| Days after treatment | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| Initial concn. | 0.48 | | 5.20 | | 2.22 | | 54.60 | |
| 0 | 100.00 | 0.00 | 100.00 | 0.00 | 100.00 | 0.00 | 100.00 | 0.00 |
| 1 | | | | | 53.67 | 1.69 | 68.78 | 3.85 |
| 3 | 20.24 | 0.21 | 43.03 | 4.14 | 30.06 | 6.33 | 54.55 | 5.92 |
| 5 | | | | | 17.58 | 1.71 | 33.49 | 9.95 |
| 8 | 6.79 | 0.13 | 13.29 | 0.67 | 7.16 | 3.43 | 18.49 | 5.12 |
| 12 | | | | | 3.29 | 0.67 | 12.57 | 4.23 |
| 15 | | | 0.75 | 0.02 | | | | |
| 22 | | | | | 2.65 | 0.73 | 2.74 | 1.97 |
| 23 | | | 0.63 | 0.03 | | | | |
| 34 | | | | | 2.10 | 0.71 | 0.48 | 0.20 |
| 61 | | | | | | | 0.09 | 0.02 |
| 94 | | | | | | | 0.08 | 0.01 |

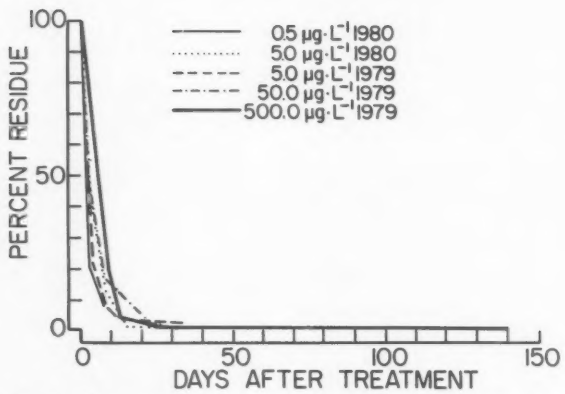


FIG. 3. Mean concentration of permethrin in limnocorrals treated with nominal concentrations of 0.5, 5, 50, and 500 $\mu g \cdot L^{-1}$ in the summers of 1979 and 1980 expressed as percent of applied material.

limnocorrals of 5.71, 5.23, and 4.68 $\mu g \cdot L^{-1}$ decreasing over 23 d to 0.036, 0.030, and 0.032 $\mu g \cdot L^{-1}$, respectively. Corrals treated at a rate of 0.5 $\mu g \cdot L^{-1}$ showed initial concentrations in the three limnocorrals of 0.48, 0.47, and 0.48 $\mu g \cdot L^{-1}$ decreasing to 0.034, 0.031, and 0.036 $\mu g \cdot L^{-1}$, respectively, after only 8 d. Dissipation of cypermethrin from small enclosures appeared to be somewhat slower, although observations were only made up to 96 h post-treatment (Shires 1983). Dissipation curves for permethrin at all concentrations used were similar (Fig. 3). Rates of dissipation were quite rapid, probably as a result of the high pH of the lake water which affects the rate of chemical hydrolysis of permethrin in laboratory experiments (Sharom and Solomon 1982). The relatively small standard errors of the residue data (Table 3) point to the good replication in this system, although the initial concentrations were not always as close to the nominal values as might be expected. The latter problem was most probably due to the difficulty in calculating the exact volume of the limnocorrals.

The lack of a linear relationship in Fig. 2 shows that the dissipation of permethrin did not fit a first-order reaction kinetics model very well and that higher order kinetics is indicated. The early phase was probably the result of chemical and biological degradation occurring simultaneously to adsorption to the sediments and sides of the limnocorral. The slower phase of dissipation may be due to a slow desorption from sediments and sides coupled with chemical and biological degradation. Adsorption to the sides of the corral is probably an important factor in the dissipation of permethrin from the water column. Due to limitations in analytical equipment, it was not possible to measure adsorption to the sides of the corrals directly, or indirectly from adsorption constants (Sharom and Solomon 1981a). Shires (1983) showed that only 2% of cypermethrin applied at 50 $g \cdot ha^{-1}$ to 1 $m^3$ was adsorbed to the stainless steel sides. However, subsequent studies on methoxychlor have shown adsorption to the sides to account for 25% of the applied pesticide (K. R. Solomon, J. Y. Yoo, D. Lean, N. K. Kaushik, K. E. Day, and G. L. Stephenson, in preparation). Earlier studies in lake water (Sharom and Solomon 1982) indicated the importance of biological degradation in the process of dissipation, and it seemed most likely that this was a result of microbial and/or algal activity because most of the zooplankton were killed by the permethrin. In an attempt to quantify the dissipation of permethrin in the system, the residue data from the first 8–19 d were fitted to a first-order reaction kinetic model (Table 4). While the fit of the data to this model is not excellent, the half-life of permethrin in the system was relatively short at 2–4 d. Likewise the time to 90% dissipation (DT90) was also relatively short at 13–27 d. Use of a polynomial regression (Table 4) gave a better description of the observed data up to about 10 d post-treatment with half-lives similar to those above and DT90 values of 3.65–9.1 d, which were more in line with field observations. Rawn et al. (1982), in similar studies with $^{14}C$-labelled permethrin in artificial ponds, also showed non-first-order dissipation and a half-life of the order of 5–8 d. Dissipation in our limnocorrals appeared to be more rapid but the pH of the water (not reported by Rawn et al. 1982) may have been different enough to account for this.

The sediment samples rapidly accumulated permethrin, and

TABLE 4. Permethrin dissipation times at different concentrations using a first-order kinetic model and a polynomial regression.

| Year | Concentration ($\mu g \cdot L^{-1}$) | Time interval (d) | Rate ($d^{-1}$) | $t_{0.5}$ (d) | $t_{0.9}$ (d) | $r^2$ [f] |
|---|---|---|---|---|---|---|
| 80 | 0.5 | 0–8[a] | 0.335 | 2.1 | 13.8 | 0.747 |
| | | All[b] | — | 1.65 | 3.65 | 1 |
| 80 | 5.0 | 0–15[a] | 0.325 | 2.1 | 14.2 | 0.795 |
| | | All[c] | — | 3.7 | 9.1 | 0.94 |
| 79 | 5.0 | 0–12[a] | 0.313 | 2.2 | 14.7 | 0.749 |
| | | All[d] | — | 1.85 | 5.7 | 0.96 |
| 79 | 50.0 | 0–8[a] | 0.206 | 3.4 | 22.4 | 0.916 |
| | | 0–12[a] | 0.170 | 4.1 | 27.1 | 0.852 |
| | | All[e] | — | 3.5 | 6.67 | 0.96 |
| 79 | 500.0 | 0–12[a] | 0.262 | 2.7 | 17.6 | 0.977 |
| | | 0–19[a] | 0.208 | 3.3 | 22.1 | 0.856 |

[a]First-order kinetic model: equation of the form $2.303 \log [A]/[A^0] = -kt$.

[b]Polynomial regression line of best fit: $Y = 100 - 35.5X + 2.98X^2$.

[c]Polynomial regression line of best fit: $Y = 89.5 - 12X + 0.36X^2$.

[d]Polynomial regression line of best fit: $Y = 90.6 - 27.2X + 2.88X^2 - 0.119X^3 + 0.0016X^4$.

[e]Polynomial regression line of best fit: $Y = 87 - 11.3X + 0.46X^2 - 0.07X^3 + 0.000036X^4$.

[f]Correlation coefficient determined from a least-squares regression analysis of the transformed data or a polynomial regression of the untransformed data.

TABLE 5. Permethrin concentration (mg·kg dry mass$^{-1}$) in sediments from limnocorrals treated in 1979 (upper = upper 2.5 cm; lower = rest of the cup).

| Days after treatment | Limnocorral (50 $\mu g \cdot L^{-1}$) Position | 3 | 7 | 12 | Mean ± SD |
|---|---|---|---|---|---|
| 8 | Upper | 17.53 | 16.75 | 16.63 | 16.97±0.40 |
| | Lower | 0.146 | 0.144 | 0.169 | 0.153±0.01 |
| 12 | Upper | 11.55 | 14.32 | 18.66 | 14.84±2.9 |
| | Lower | 0.196 | 0.348 | | |
| 22 | Upper | 16.64 | 10.46 | 13.20 | 13.43±2.53 |
| | Lower | 0.369 | 0.286 | 0.353 | 0.336±0.036 |
| 34 | Upper | 11.53 | 11.10 | 12.63 | 11.75±0.641 |
| | Lower | 0.277 | 0.196 | 0.389 | 0.287±0.079 |

| Days after treatment | Limnocorral (5.0 $\mu g \cdot L^{-1}$) Position | 2 | 6 | 8 | Mean ± SD |
|---|---|---|---|---|---|
| 8 | Upper | 2.29 | 2.02 | 2.20 | 2.17±0.111 |
| | Lower | 0.177 | 0.133 | 0.135 | 0.148±0.020 |
| 12 | Upper | 1.24 | 1.31 | 1.62 | 1.34±0.165 |
| | Lower | 0.196 | 0.196 | 0.130 | 0.173±0.031 |
| 22 | Upper | 1.03 | 0.95 | 1.28 | 1.08±0.142 |
| | Lower | 0.341 | 0.362 | 0.266 | 0.323±0.041 |
| 34 | Upper | 1.13 | 1.02 | 1.04 | 1.06±0.048 |
| | Lower | 0.309 | 0.261 | 0.194 | 0.255±0.047 |

slowly dissipated it over the time of observation (Table 5). These trends are similar to those reported by Sharom and Solomon (1981b) from laboratory studies using the same sediments and from field results in artificial ponds (Rawn et al. 1982) and are consistent with a high affinity of permethrin for sediments, slow release of the pesticide, followed by a more rapid degradation in solution. The amounts released are probably not biologically significant to animals in the water column: however, sediment-dwelling organisms such as reported for nymphs of the burrowing mayfly (Friesen et al. 1983) may be affected. Very few benthic organisms were present in the Lake St. George sediments and no observations of toxicity could be made (Kaushik et al. 1985). There was very little penetration of permethrin into the sediments as was indicated by the concentrations in the lower parts of the cups. Sharom and Solomon (1981b) have shown similar low penetration rates in laboratory studies on the same sediments.

Limnocorrals and enclosures have been quite widely used for studying the effects of a number of chemicals in the aquatic environment but this study is the first in which a pesticide has been used. The results obtained show that the limnocorral is a suitable method for the study of a number of chemical effects of pesticides in aquatic systems. The dissipation of the pesticide, its adsorption by sediments, and other components of the system may be determined under more natural conditions than are attainable in the laboratory and these observations may be made in replicate enclosures, thus adding more certainty to predictions based on the results obtained. In addition to chemical information, the limnocorral also allows the investigation of the direct effects (lethal toxicity, reduction of growth and reproduction, behavioural changes, etc.) and indirect effects (community interactions as reflected by diversity, productivity, and changes in species composition and abundance) on natural communities. Kaushik et al. (1985) have shown good intraseasonal replication of effects among similarly treated corrals, and despite a 60-d difference in time of application of permethrin in 1979 and 1980, interseasonal replication of effects were noted at 5 $\mu g \cdot L^{-1}$. The use of limnocorrals also enables replicate treatments on communities similar to those occurring in the lake without the need to contaminate the entire lake with pesticides.

As in any field bioassay system, the costs are also of importance. The capital and installation cost of a 125-$m^3$ corral is approximately $2400 (Cdn), and with an expected useful life of seven seasons, this is comparable with an artificial pond system of similar size, less expensive than a similar concrete pond, and much less expensive than a similar sized laboratory system. Chemical analysis and enumeration of the biological effects are labour intensive and represent about 80% of the total costs of such studies; however, these costs would be the same for equally comprehensive studies in other forms of container. The system does have a number of disadvantages such as difficulty of sampling and adsorption of lipid soluble pesticides to the walls, but these can, for the most part, be overcome or at least measured and taken into account. On balance, the limnocorral offers more replicatability, repeatability, and realism than other systems and will become a useful tool for studying the effects of pesticides in aquatic systems.

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## References


ALI, A., AND M. S. MULLA. 1978. Effects of chironomid larvicides and diflubenzuron on nontarget invertebrates in residual–recreational lakes. Environ. Entomol. 7: 21–27.

ANDERSON, R. S. 1970. Effects of rotenone on zooplankton communities and a study of their recovery patterns in two mountain lakes in Alberta. J. Fish. Res. Board Can. 27: 1335–1356.

BCPC. 1979. The pesticide manual. A world compendium. 6th ed. C. R. Worthing [ed.] British Crop Protection Council, 655 p.

BEERS, J. R., M. R. REEVE, AND G. D. GRICE. 1977. Controlled ecosystem pollution experiment. Effects of mercury on enclosed water columns. IV. Zooplankton population dynamics and production. Mar. Sci. Comm. 3: 355–394.

BLINN, D. W., T. TOMPKINS, AND L. ZALESKI. 1977. Mercury inhibition of primary productivity using large volume plastic enclosures *in situ*. J. Phycol. 13: 58–61.

BOYCE, F. M. 1974. Mixing within experimental enclosures: a cautionary note on the limnocorral. J. Fish. Res. Board Can. 31: 1400–1405.

CROSSLAND, N. O. 1982. Aquatic toxicology of cypermethrin. II. Fate and biological effects in pond experiments. Aquat. Toxicol. 2: 205–222.

CROSSLAND, N. O., S. W. SHIRES, AND D. BENNETT. 1982. Aquatic toxicology of cypermethrin. III. Fate and biological effects of spray drift deposits in fresh water adjacent to agricultural land. Aquat. Toxicol. 2: 253–270.

DAVIES, J. M., AND J. C. GAMBLE. 1979. Experiments with large enclosed ecosystems. Philos. Trans. R. Soc. Lond. B Biol. Sci. 286: 523–544.

DRAGGAN, S. 1976a. The role of microcosms in ecological research (an introduction to this special issue on microcosms). Int. J. Environ. Stud. 10: 1–2.

1976b. The microcosm as a tool for estimation of environmental transport of toxic materials. Int. J. Environ. Stud. 10: 65–70.

ENVIRONMENT CANADA. 1979. Analytical methods manual, Ottawa, Ont. 267 p.

FRIESEN, M. K., T. D. GALLOWAY, AND J. F. FLANNAGAN. 1983. Toxicity of the insecticide permethrin to nymphs of the burrowing mayfly *Hexagenia rigida* (Ephermeroptera: Ephimeridae). Can. Entomol. 115: 1007–1014.

HUGHES, D. N., M. G. BOYER, M. H. PAPST, AND C. D. FOWLE. 1980. Persistence of three organophosphorus insecticides and some biological implications. Arch. Environ. Contam. Toxicol. 9: 269–279.

HURLBERT, S. H., M. S. MULLA, AND H. R. WILSON. 1972. Effects of an organophosphorus insecticide on the phytoplankton, zooplankton and insect population of fresh water ponds. Ecol. Monogr. 42: 269–299.

KAUSHIK, N. K., G. L. STEPHENSON, K. R. SOLOMON, AND K. E. DAY. 1985. Impact of permethrin on zooplankton communities in limnocorrals. Can. J. Fish. Aquat. Sci. 42: 77–85.

KINGSBURY, P. D. 1976. Effects of an aerial application of the synthetic pyrethroid permethrin on a forest stream. Manit. Entomol. 10: 9–17.

KUIPER, J. 1977. An experimental approach in studying the influence of mercury on a North Sea coastal plankton community. Helgol. Wiss. Meeresunters. 30: 652–665.

1981. Fate and effects of mercury in marine plankton communities in experimental enclosures. Ecotoxicol. Environ. Saf. 5: 106–134.

LACK, T. J., AND W. G. LUND. 1974. Observations and experiments on the phytoplankton of Blelham Tarn, English Lake District. Freshwater Biol. 4: 399–415.

LEAH, R. T., B. MOSS, AND D. E. FORREST. 1978. Experiments with large enclosures in a fertile, shallow, brackish lake, Hickling Broad, Norfolk, United Kingdom. Int. Rev. Gesamten Hydrobiol. 63: 291–310.

MARSHALL, J. S., AND D. L. MELLINGER. 1980. An *in situ* experimental method for toxicological studies on natural plankton communities, p. 27–39. *In* J. G. Eaton, P. R. Parish, and A. C. Hendricks [ed.] Aquatic toxicology. ASTM STP 707. American Society for Testing and Materials, Philadelphia, PA.

MENZEL, D. W., AND J. CASE. 1977. Concept and design: controlled ecosystem pollution experiment. Bull. Mar. Sci. 27: 1–7.

METCALF, R. L., G. K. SANGHA, AND I. P. KAPOOR. 1971. Model ecosystem for the evaluation of pesticide biodegradability and ecological magnification. Environ. Sci. Technol. 5: 709–713.

RAWN, G. P., G. R. B. WEBSTER, AND D. C. G. MUIR. 1982. Fate of permethrin in model outdoor ponds. J. Environ. Health Sci. B17: 463–486.

SHAROM, M. S., AND K. R. SOLOMON. 1981a. Adsorption and desorption of permethrin and other pesticides on glass and plastic materials used in bioassay procedures. Can. J. Fish. Aquat. Sci. 38: 199–204.

1981b. Adsorption–desorption, degradation and distribution of permethrin in aqueous systems. J. Agric. Food Chem. 29: 1122–1125.

1982. The influence of adsorption on glass, pH and temperature of the disappearance of permethrin in aqueous systems. Environ. Pollut. Ser. B Chem. Phys. 4: 269–279.

SHIRES, S. W. 1983. The use of small enclosures to assess the toxic effects of cypermethrin in fish under field conditions. Pestic. Sci. 14: 475–480.

SOLOMON, K. R., K. E. SMITH, G. GUEST, J. YOO, AND N. K. KAUSHIK. 1980. The use of limnocorrals in studying the effects of pesticides in the aquatic ecosystem. Can. Tech. Rep. Fish. Aquat. Sci. 975: 1–9.

SOLOMON, K. R., K. E. SMITH, AND G. L. STEPHENSON. 1982. Depth integrating samplers for use in limnocorrals. Hydrobiologia 94: 71–75.

STEPHENSON, R. R. 1982. Aquatic toxicity of cypermethrin. I. Acute toxicity to some freshwater fish and invertebrates in laboratory tests. Aquat. Toxicol. 2: 175–185.

STRATTON, G. W., AND C. T. CORKE. 1981. Interaction between acetone and two pesticides towards several unicellular green algae. Bull. Environ. Contam. Toxicol. 27: 13–16.

TAUB, F. B. 1976. Demonstration of pollution effects in aquatic microcosms. Int. J. Environ. Stud. 10: 23–33.

TWINCH, A. J., AND C. M. BREEN. 1981. The thermal, oxygen and light regimes in isolated columns of water in a turbid impoundment. Freshwater Biol. 10: 207–213.

# Impact of Permethrin on Zooplankton Communities in Limnocorrals

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Kaushik, N. K., G. L. Stephenson, K. R. Solomon, and K. E. Day. 1985. Impact of permethrin on zooplankton communities in limnocorrals. Can. J. Fish. Aquat. Sci. 42: 77–85.

A series of in situ aquatic enclosures or limnocorrals (5 × 5 × 5 m deep) was used to evaluate the impact of the insecticide permethrin (3-phenoxybenzyl(1RS)-*cis*,*trans*-3-(2,2-dimethyl-3-dichlorovinyl)-2,2-dimethylcyclopropanecarboxylate) (50.0 and 5.0 $\mu g \cdot L^{-1}$ in 1979 and 5.0 and 0.5 $\mu g \cdot L^{-1}$ in 1980) on the pelagic zooplankton community in a 10-ha mesotrophic lake in southern Ontario. Permethrin was acutely toxic to the macrozooplankton (Cladocera and Copepoda) at all concentrations; microzooplankton (Rotifera) showed acute toxicity only at 50.0 $\mu g \cdot L^{-1}$. Despite this initial toxicity, the density of microzooplankton increased dramatically 15–20 d post-treatment in all treated enclosures, and the rotifer populations dominated the zooplankton community for 3–4 wk. The high densities of microzooplankton were attributed to their inherent reproductive capabilities when released from competition and predation pressures. Resilience of the different zooplankton taxa was variable and depended upon both the species and the exposure concentration. Diversity of zooplankton was significantly reduced in communities exposed to permethrin. The limnocorral technique has proved to be an important tool for assessment of direct and indirect impacts of pesticides on and probable recovery of a zooplankton community under natural conditions.

Nous avons étudié in situ des secteurs (5 × 5 × 5 m de profondeur) du limnocorail d'un lac mésotrophe de 10 ha situé dans le sud de l'Ontario pour connaître les effets d'un insecticide (la perméthrine (cyclopropanecarboxylate de 3-phénoxybenzyl(1RS)-*cis*,*trans*-3-(2,2-diméthyl-3-dichlorovinyl)-2,2-diméthyle), appliquée à raison de 50,0 et 5,0 $\mu g \cdot L^{-1}$, en 1979, et de 5,0 et 0,5 $\mu g \cdot L^{-1}$, en 1980) sur le zooplancton pélagique. Nous avons constaté que la perméthrine produit un effet toxique aigu chez le macrozooplancton (Cladocera et Copepoda) à toutes les concentrations étudiées, tandis que chez le microzooplancton (Rotifera), il ne se manifeste un effet de toxicité aiguë qu'à 50,0 $\mu g \cdot L^{-1}$. En dépit de cette toxicité initiale, les populations de microzooplancton ont considérablement augmenté 15 à 20 jours après le traitement dans tous les secteurs traités ; les rotifères ont constitué l'élément dominant du zooplancton pendant 3 ou 4 sem. Nous pensons que l'abondance des organismes du microzooplancton s'explique par la fécondité qui leur est inhérente et qui s'est manifestée lorsque leurs prédateurs et leurs compétiteurs sont disparus. La résistance des divers types d'organismes zooplanctoniques variait selon l'espèce considérée et la concentration d'insecticide administrée. La diversité des espèces zooplanctoniques était réduite dans une mesure significative dans les populations traitées. L'étude du limnocoral se révèle un moyen très utile pour évaluer les effets directs et indirects des pesticides sur le zooplancton et déterminer les possibilités que les populations touchées se rétablissent en milieu naturel.

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Zooplankton constitute a very important, dynamic, and complex component of a lake ecosystem. Functionally the group includes detritivores, herbivores, carnivores, and omnivores, and all these groups are involved in nutrient cycling. Since zooplankton are linked directly with phytoplankton, on one hand, and higher organisms and fish, on the other, any impact on zooplankton is likely to influence primary as well as tertiary production. In the past, most studies on the effects of pesticides on zooplankton have concerned direct effects, or have been based on single species tests in the laboratory (Cairns 1983). Although secondary or indirect effects of pesticides have long been recognized (see Hurlbert 1975 for a review), only a few studies have reported such effects. However, with the increasing use of microcosms and mesocosms for assessing the impact of contaminants on natural communities, chances of observing such effects have increased. Studies using microcosms ($\leq 10\ m^3$ in volume, Banse 1982) generally involve simplified food chains and employ populations of only a few species. In recent years a number of papers using mesocosms ($>10\ m^3$ in volume) for assessing the impact of pollutants on aquatic communities have appeared (Banse 1982; Smies 1983). These papers (Hurlbert et al. 1972; Dortland 1980; Hughes et al. 1980) deal with zooplankton communities in shallow, artificial ponds, in land-based experimental tanks (Hodson and Millard 1978; Pilson and Nixon 1980), and in in situ enclosures. The literature contains only two reports on the impact of heavy metals on zooplankton using freshwater enclosures (Urech 1979; Marshall and Mellinger 1980). We are not aware of any published report on the impact of a pesticide on zooplankton in in situ enclosures in freshwater.

This paper describes the results of a study, carried out in 1979 and 1980, on the impact of an insecticide, permethrin, on zooplankton in limnocorrals in a southern Ontario lake.

## Materials and Methods

Details regarding design, size, construction, and installation of the limnocorrals have been described by Solomon et al. (1980). Briefly, the walls of the limnocorrals (5 × 5 × 5 m deep) were dropped and anchored firmly into the sediment, effectively isolating comparable sections of the lake ecosystem from the water surface to the lake bottom. In 1979, permethrin (3-phenoxybenzyl(1RS)-*cis*,*trans*-3-(2,2-dimethyl-3-dichlorovinyl)-2,2-dimethylcyclopropanecarboxylate) was applied on 15 and 16 August to the limnocorrals to obtain a nominal concentration of 5 $\mu g \cdot L^{-1}$ in three corrals and 50 $\mu g \cdot L^{-1}$ in another set of three. The remaining three corrals served as controls and were treated with 0.5 L of acetone, used as a solvent for the pesticide. Details regarding application and degradation of the pesticide and water chemistry have been reported in a concurrent study by Solomon et al. (1985) who used the same corrals. Three open-water stations and all enclosures were sampled weekly from 1 August to 20 November 1979. Duplicate zooplankton samples were collected from the centre of each enclosure at depths of 0.5, 1.5, 2.5, and 3.5 m with a 15-L Schindler–Patalas plankton trap fitted with 30-μm Nytex mesh. The zooplankton samples were preserved immediately with a 4% sucrose formalin solution (Haney and Hall 1973). In the laboratory, 1- and 5-mL subsamples for microzooplankton and macrozooplankton, respectively, were pipetted onto counting chambers and using both compound and dissecting microscopes the organisms were counted and identified using Edmondson (1959), Chengalath et al. (1971), Brandlova et al. (1972), Grothe and Grothe (1977), Smith and Fernando (1978), and Pennak (1978). A minimum of 300 individuals of the most common species was counted. This usually entailed counting one to five subsamples. The whole sample was counted when plankton densities were <300 individuals per sample.

In 1980, the pretreatment period extended from 27 May to 9 June. Permethrin was applied on 10 and 11 June to give nominal concentrations of 5.0 $\mu g \cdot L^{-1}$ in three corrals and 0.5 $\mu g \cdot L^{-1}$ in another set of three corrals, and the post-treatment period extended to 23 September. Because in 1979 the variation between estimations of zooplankton density for samples taken at different depths was greater than the variation between replicate estimates within a given depth, a vertically integrating 150-mm-OD tube sampler (Solomon et al. 1982) was used for the weekly collection of three zooplankton samples from each enclosure and each outside station. The integrating tube sampler expedited the sampling process and also reduced the laboratory counting load. Each sample was preserved in formalin. The macrozooplankton (Cladocera and Copepoda) were identified and enumerated in a modified counting wheel (Ward 1955) with a stereo microscope. The microzooplankton (Rotifera) were identified and enumerated in a Sedgewick Rafter Cell with a compound microscope.

Criteria used to evaluate the impact of permethrin on the enclosed zooplankton were density, species diversity, and relative percentage abundance. The density (number of organisms per unit volume) of individual species and of groups of species in the permethrin-treated limnocorrals was compared with that in the controls by simply graphing the mean densities of replicate treatments over time. For statistical evaluation of the impact of permethrin on density of individual species of zooplankton, a standard *t*-test was performed on the means of log $(x + 1)$ transformed data of controls and each treatment. Where the variances were significantly different (determined by *F*-test) the degrees of freedom were adjusted using Sutterthwaite's approximation (Steele and Torrie 1960).

Shannon–Weaver diversity indices were calculated for the pelagic zooplankton in treated and control enclosures on each 1980 sampling date using the formula

$$H' = -\sum_{i=1}^{s} p_i \log p_i$$

where $s$ is the number of species and $P_i$ is the proportion of total number of individuals consisting of the $i$ species (Poole 1974). The pelagic zooplankton were divided into six groups: (1) Cladocera, (2) Calanoida, (3) Cyclopoida, (4) copepod nauplii, (5) copepod copepodites, and (6) Rotifera. A weekly comparison of the relative percentage abundances of these groups for 1980 was made between the control limnocorrals and treated enclosures.

## Results

While macrozooplankton densities in the control corrals and at the outside stations were similar during the study period, there was a dramatic numerical decrease in treated enclosures soon after the application of 5.0 or 50.0 μg permethrin·$L^{-1}$ (Fig. 1). The outside stations have been included to show the similarity of the control enclosures to the natural lake, but only the control corrals were used for impact assessment of permethrin. Similar results were obtained in 1980 even though the permethrin concentrations in the treated corrals were 0.5 or 5.0 $\mu g \cdot L^{-1}$ and the treatment was applied on 10 and 11 June, as opposed to 15 and 16 August during 1979. Cladocera were more numerous than the copepod groups in 1980 (Fig. 2) in all corrals before application of the pesticide and in the control corrals throughout the experiment. However, both concentrations (5.0 and 0.5 $\mu g \cdot L^{-1}$) of permethrin in 1980 had a pronounced effect on the three major groups of Crustacea as well as the nauplii and copepodite populations (Fig. 2).

No macrozooplankton species increased in number when exposed to permethrin; however, some species were obviously more resilient than others (Table 1). For example, *Daphnia galeata mentotae*, *Daphnia ambigua*, and *Bosmina longirostris* were not significantly reduced in numbers when exposed to 0.5 μg permethrin·$L^{-1}$. The 5.0 μg permethrin·$L^{-1}$ concentration did not significantly reduce the numbers of *D. g. mendotae*, but *D. ambigua* expressed a significant numerical reduction at day 22 and *B. longirostris* at day 15 and day 22 (Table 1). Conversely, *Ceriodaphnia lacustris*, *Diaptomus oregonensis*, *Tropocyclops prasinus mexicanus*, and the immature copepod stages exhibited less resilience to the pesticide in that recovery from the initial toxicity was between days 35 and 42 (Table 1).

Although the crustacean populations in corrals treated during 1979 began to increase by about 15 d post-treatment, recovery of these organisms in corrals treated with 5.0 μg permethrin·$L^{-1}$ to control levels did not occur until 40–60 d after the treatment (Fig. 1). In corrals treated with 50.0 μg permethrin·$L^{-1}$, recovery was much slower, and in fact, numbers comparable with controls were not attained until the spring of the following year. Similar trends for recovery of crustacean populations were recorded in 1980 (Fig. 2). Recovery of the

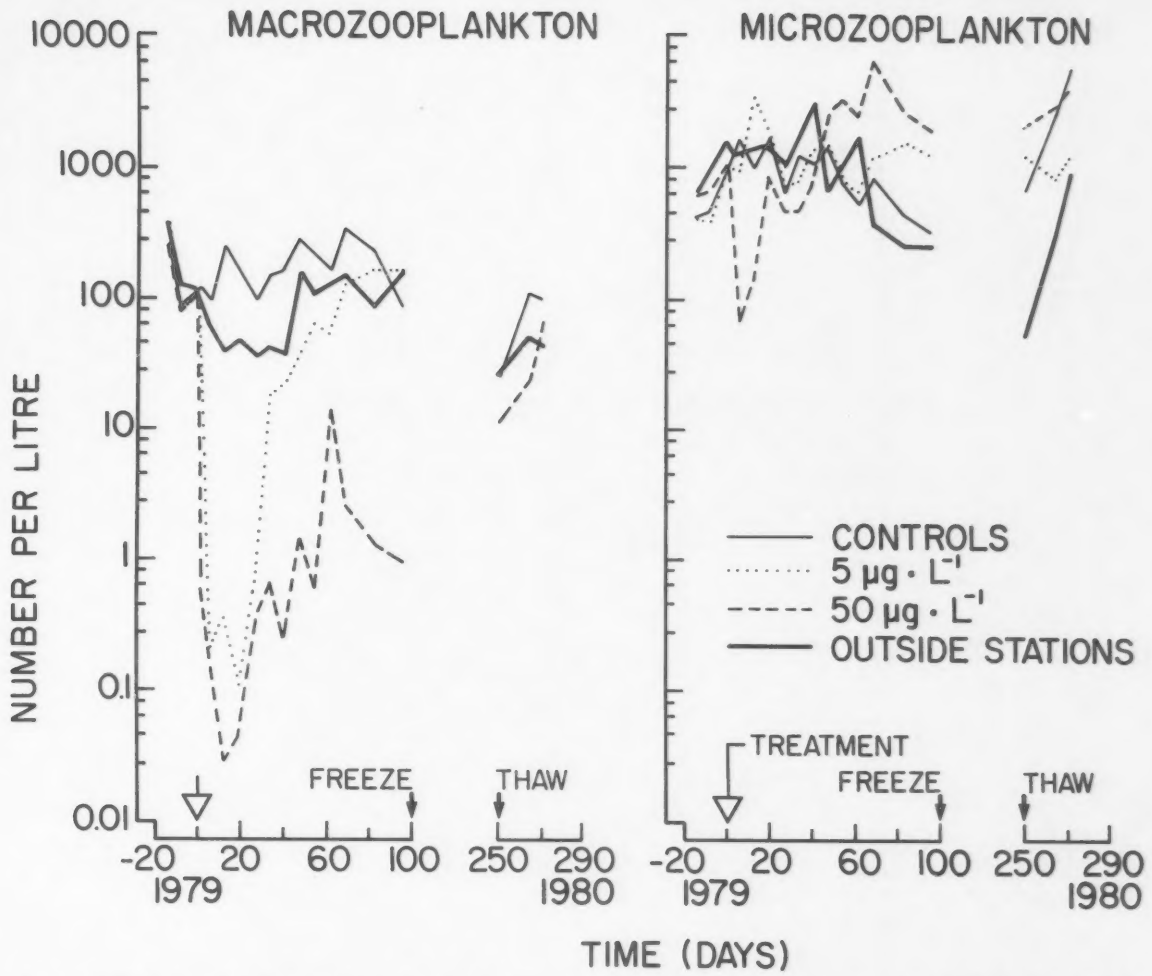


FIG. 1. Changes in mean densities of macrozooplankton and microzooplankton in control limnocorrals, limnocorrals treated with permethrin, and at outside stations (open lake) in 1979.

Cladocera started about 20 d after application of the pesticide, and in both permethrin concentrations (0.5 and 5.0 $\mu g \cdot L^{-1}$), populations similar to those in controls were reached by 40–50 d post-treatment. Recovery of copepods appeared to be more gradual, but by day 50 their density was similar to that in controls. This is also the case for nauplii and copepodite populations.

During 1979, rotifer densities in corrals treated with 50 µg permethrin $\cdot L^{-1}$ declined slightly but the impact was short-lived and not as dramatic as that observed for crustacea (Fig. 1). Numbers of rotifers promptly recovered from this initial setback and then maintained populations very close to or much higher than those in controls. In corrals with 5 µg permethrin $\cdot L^{-1}$, there was an increase in numbers which persisted for about 20 d. During 1980, the numerical response of rotifers was the same for both the concentrations, and as noted in the 1979 5.0 µg permethrin $\cdot L^{-1}$ treatment, there was a dramatic increase in numbers starting about 10 d after application of the pesticide (Fig. 2). The numbers peaked at day 22, with densities as high as 4500–5000 organisms $\cdot L^{-1}$ compared with a population of only about 1000 $\cdot L^{-1}$ before treatment. Rotifer numbers returned to control levels by day 40 post-treatment.

To determine whether the permethrin treatment resulted in increased densities of all species of rotifers or that of selected taxa, species comprising ≥90% of the rotifer populations in control corrals in 1980 were compared with those in 0.5 and 5.0 µg permethrin $\cdot L^{-1}$ treated corrals for each sampling date (Table 1). No significant difference was noted for *Keratella quadrata* on any of the sampling days. *Trichocerca multicrunus*, *Conochilus unicornis*, and *Kellicottia longispina* showed significant increases on a number of occasions. However, the greatest change was noticed for *Keratella cochlearis* and *Polyarthra* spp., which increased significantly for seven and three consecutive weeks, respectively, in corrals treated with 5.0 µg permethrin $\cdot L^{-1}$. None of the rotifer species in the treated corrals differed significantly in abundance from that in the control corrals after 77 d.

Figure 3 clearly shows the effect of permethrin on the mean relative percentage abundances of the six zooplankton groups as well as apparent recovery to control levels. The communities in

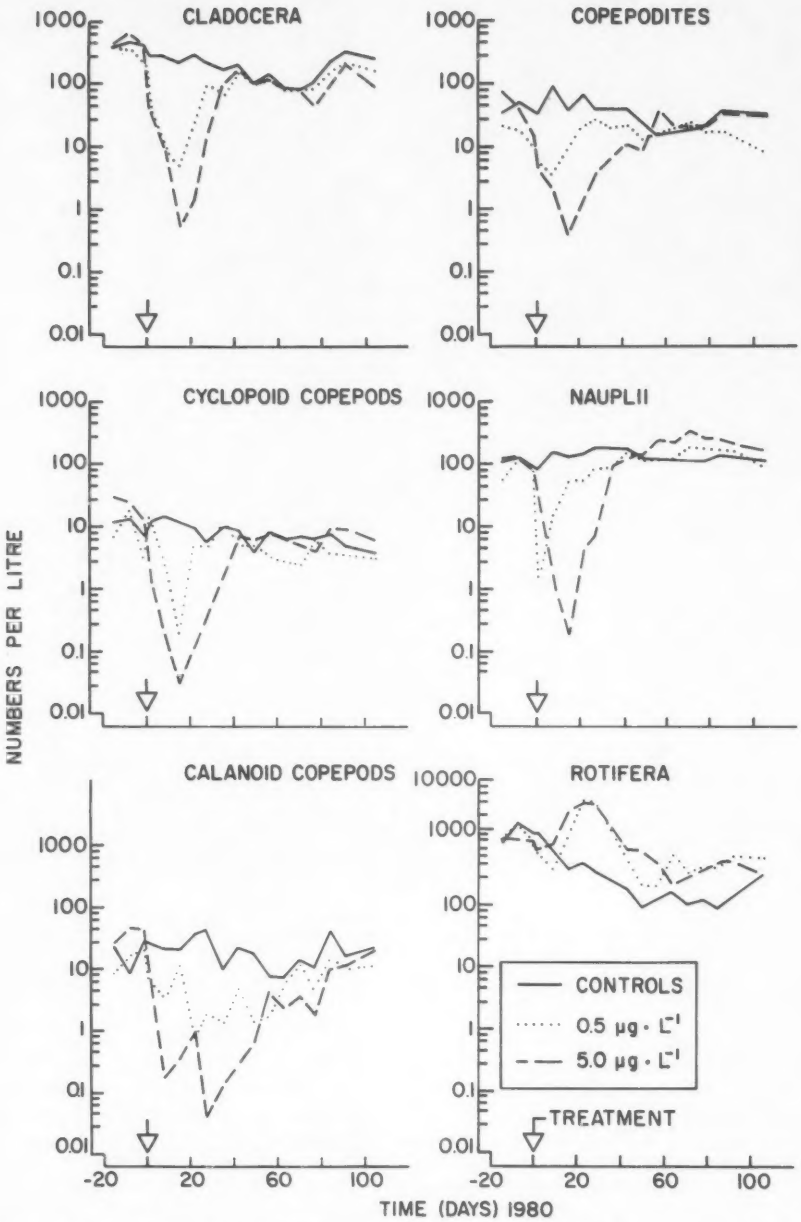


FIG. 2. Changes in mean densities of the major macrozooplankton groups and microzooplankton in control and permethrin-treated limnocorrals in 1980.

all the enclosures were similar before addition of the pesticides. Immediately post-treatment (e.g. day 1) there was a dramatic decline in the relative abundance of all groups exposed to permethrin except rotifers, which increased proportionally and dominated the community for the next 6 wk. The community composition remained surprisingly "stable" in the control corrals over the season. The differential rate of recovery exhibited by the zooplankton groups exposed to permethrin reflected the greater impact of the higher concentration. Recovery of the affected macrozooplankton to near control levels correlated with a decrease in the relative dominance of rotifers in the community.

## Discussion

Laboratory testing has shown that synthetic pyrethroids have a high acute toxicity to aquatic organisms (Jolly et al. 1978; Muirhead-Thomson 1977; McLeese et al. 1980; Stephenson

TABLE 1. Post-treatment sampling days in 1980 on which the mean of transformed counts for the most common species in enclosures treated with permethrin differed significantly from those in the control enclosures (−, decrease; +, increase). *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; NSD, no significant difference.

| Species | Treatment means ± SE of transformed counts | | | Post-treatment sampling day | |
|---|---|---|---|---|---|
| | Control | 0.5 μg·L$^{-1}$ | 5.0 μg·L$^{-1}$ | 0.5 μg·L$^{-1}$ | 5.0 μg·L$^{-1}$ |
| Cladocera | | | | | |
| *Daphnia g. mendotae* | — | NSD | NSD | — | — |
| *Daphnia ambigua* | 0.661±0.083 | NSD | 0 | — | (−) 22** |
| *Diaphanosoma brachyurum* | 0.602±0.246 | 0 | 0 | (−) 15* | (−) 15* |
| | 0.583±0.223 | 0 | 0 | (−) 22* | (−) 22* |
| *Ceriodaphnia lacustris* | 1.637±0.497 | 0.297±0.367 | NSD | (−) 1** | — |
| | 1.805±0.394 | 0.126±0.286 | 0.163±0.320 | (−) 8** | (−) 8** |
| | 1.810±0.077 | 0.026±0.061 | 0 | (−) 15*** | (−) 15*** |
| | 1.802±0.763 | NSD | 0 | — | (−) 22* |
| | 1.993±0.373 | 0.333±0.332 | 0.077±0.275 | (−) 27** | (−) 27** |
| | 1.861±0.314 | 0.653±0.402 | 0.201±0.299 | (−) 35* | (−) 35* |
| *Bosmina longirostris* | 1.649±0.635 | NSD | 0.157±0.455 | — | (−) 15* |
| | 1.785±0.463 | NSD | 0.273±0.390 | — | (−) 22* |
| *Chydorus sphaericus* | 1.242±0.482 | 0.208±0.369 | NSD | (−) 8* | — |
| | 1.023±0.403 | 0.100±0.302 | 0 | (−) 15* | (−) 15* |
| Copepoda | | | | | |
| Calanoida | | | | | |
| *Diaptomus oregonensis* | 1.293±0.192 | NSD | 0.060±0.147 | — | (−) 8** |
| | 1.233±0.282 | NSD | 0.106±0.222 | — | (−) 15** |
| | 1.562±0.096 | 0.159±0.173 | 0.205±0.210 | (−) 22** | (−) 22** |
| | 1.594±0.207 | 0.336±0.273 | 0.015±0.147 | (−) 27* | (−) 27*** |
| | 0.907±0.294 | NSD | 0.049±0.213 | — | (−) 35* |
| Cyclopoida | | | | | |
| *Tropocyclops p. mexicanus* | 0.793±0.163 | 0.170±0.152 | 0.003±0.115 | (−) 8* | (−) 8* |
| | 0.560±0.059 | 0.038±0.056 | 0.004±0.042 | (−) 15*** | (−) 15** |
| | 0.477±0.000 | NSD | 0.085±0.085 | — | (−) 27* |
| *Mesocyclops edax* | 0.719±0.179 | NSD | 0 | — | (−) 35** |
| | 0.593±0.091 | 0.201±0.119 | 0.028±0.066 | (−) 42* | (−) 42** |
| Immature stages | | | | | |
| Nauplii | 1.891±0.103 | 0.350±0.116 | NSD | (−) 1*** | — |
| | 2.156±0.174 | 1.020±0.380 | 0.229±0.237 | (−) 8* | (−) 8** |
| | 2.115±0.010 | NSD | 0.068±0.040 | — | (−) 15*** |
| | 2.161±0.019 | NSD | 0.435±0.356 | — | (−) 22** |
| | 2.260±0.089 | NSD | 0.626±0.372 | — | (−) 27* |
| | 2.260±0.071 | 1.945±0.068 | NSD | (−) 35** | — |
| Copepodites | 1.935±0.196 | 0.560±0.253 | 0.293±0.309 | (−) 8* | (−) 8** |
| | 1.577±0.127 | NSD | 0.116±0.129 | — | (−) 15*** |
| | 1.800±0.201 | NSD | 0.269±0.258 | — | (−) 22** |
| | 1.486±0.310 | NSD | 0.408±0.369 | — | (−) 27* |
| Rotifera | | | | | |
| *Keratella quadrata* | — | NSD | NSD | — | — |
| *Trichocercus multicrinus* | 0.634±0.250 | NSD | 1.703±0.280 | — | (−) 22* |
| | 0.360±0.259 | 1.412±0.205 | NSD | (+) 27** | — |
| *Conochilus unicornis* | 0.201±0.284 | NSD | 1.802±0.360 | — | (+) 49* |
| | 0.107±0.077 | 0.852±0.178 | 1.319±0.222 | (+) 56* | (+) 56* |
| *Kellicottia longispina* | 0.134±0.041 | 0 | 0 | (+) 49* | (+) 49* |
| *Keratella cochlearis* | 1.626±0.197 | 2.752±0.280 | 2.690±0.231 | (+) 22* | (+) 22** |
| | 1.318±0.364 | 3.098±0.463 | 2.631±0.292 | (+) 27* | (+) 27* |
| | 1.175±0.337 | NSD | 2.466±0.389 | — | (+) 42* |
| | 0.725±0.460 | NSD | 2.256±0.443 | — | (+) 49* |
| | 0.996±0.212 | NSD | 2.177±0.167 | — | (+) 56** |
| | 1.218±0.190 | NSD | 1.878±0.147 | — | (+) 70* |
| | 1.234±0.230 | NSD | 1.791±0.194 | — | (+) 77* |
| *Polyarthra* spp. | 1.986±0.246 | NSD | 3.343±0.247 | — | (+) 15** |
| | 2.240±0.019 | 3.552±0.157 | 3.538±0.109 | (+) 22* | (+) 22** |
| | 2.393±0.289 | NSD | 3.492±0.285 | — | (+) 27* |

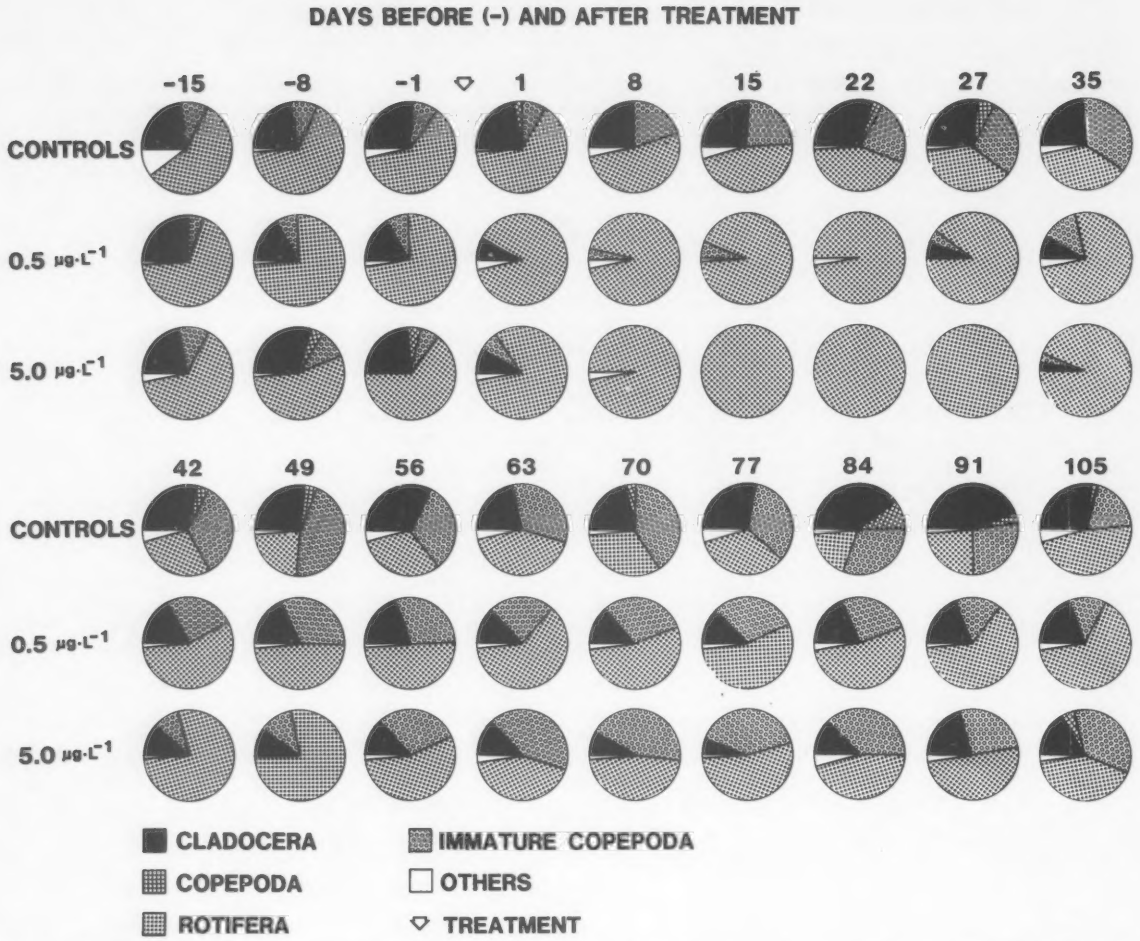


FIG. 3. Changes in relative percent abundances of major taxonomic groups in the zooplankton community in control and permethrin-treated enclosures in 1980.

1982). However, our field testing using limnocorrals showed that zooplankton population responses appear to be the result of both direct acute lethal toxicity to and indirect effects of permethrin on community dynamics. Permethrin was acutely toxic to the macrozooplankton at all concentrations, and like Kingsbury (1976) we observed both cladocera and copepod crustaceans to be susceptible to the impact of operational concentrations of permethrin. Differential rates of recovery to control levels for the various zooplankton species enabled the less resilient "indicator" species as well as the more tolerant species to be identified. *Daphnia g. mendotae* and *D. ambigua* appeared to be unaffected by permethrin. *Bosmina longirostris* was affected by the high permethrin concentration only with recovery by the fourth week (Table 1). On the other hand, numbers of *C. lacustris* and *D. oregonensis* decreased almost immediately and required the longest recovery time after exposure to permethrin and could therefore be regarded as "indicator" species.

The microzooplankton showed little sensitivity when exposed to permethrin, with the exception of the high ($50.0\,\mu g \cdot L^{-1}$) concentration (Fig. 1 and 2). Subsequent laboratory studies using *Rotaria* spp. showed a 24-h acute $LC_{50}$ in excess of 10 000 mg permethrin$\cdot L^{-1}$ applied as an emulsifiable concentrate. The difference in apparent sensitivity of the two assay systems may be due to species differences as well as exposure time. However, preliminary laboratory studies of *Rotaria* spp. showed that uptake of $^{14}C$-labelled permethrin was rapid and that a concentration of about $3 \times 10^4$ times that in the water was reached in 2 h. It thus appears that the apparent absence of toxicity is not due to lack of uptake but may be due to physiological and/or chemical differences between rotifers and the other zooplankton within the aquatic community. Hurlbert et al. (1972) and Papst and Boyer (1980) noted that rotifers were less affected by organophosphorus pesticides than other zooplankton groups, and rotifer populations increased to high levels after treatment of artificial ponds. Therefore, the rapid post-treatment increase of rotifers in treated limnocorrals appeared to be an indirect effect of the pesticide. Most planktonic rotifers are omnivorous, ingesting organic particles (smaller planktonic organisms, detritus, and bacteria) of the appropriate size (Pennak 1978). They also have a high reproductive potential and would be capable of rapid population growth under

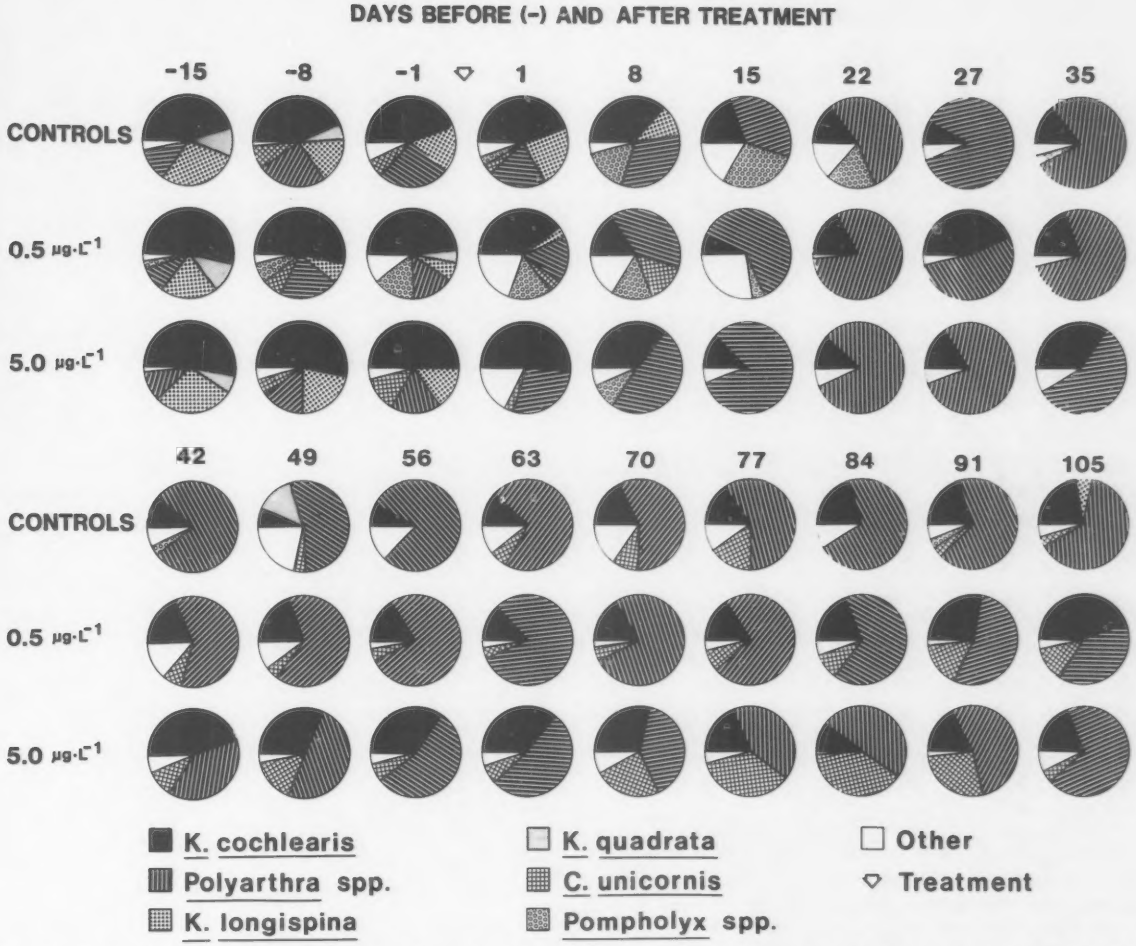


FIG. 4. Changes in relative percent abundances of the species that numerically dominate the rotifer community in control and permethrin-treated limnocorrals in 1980.

favourable conditions (Allan and Goulden 1980). The death of the larger, herbivorous, filter-feeding macrozooplankton, which consume a broad range of particle sizes, may have released the rotifers from competitive pressures for a limited supply of food. Brandl and Fernando (1978) found that rotifers are the preferred prey of at least two predator copepods (*Mesocyclops edax* and *Cyclops vicinus*), and the numerical decline of these predators as a result of exposure to permethrin may release rotifers from predation pressure. However, experimental manipulations of densities of cladoceran and copepod species by Neill (1984) in freshwater in situ enclosures produced highly significant increases in rotifer biomass only under *Daphnia* removal and not under copepod removal, which tends to attest to change in competitive pressures. In addition, an increase in numbers of bacteria, due to the decomposition of organisms killed by the pesticide, may provide an additional food source for rotifers, thus enhancing population growth. The fact that the gradual decline in numbers of rotifers coincides with the gradual recovery of the macrozooplankton (Fig. 3) supports these contentions. Miura and Takahashi (1976) conducted both laboratory and field testing of a synthetic pyrethroid at 0.2 $mg \cdot L^{-1}$ and found that copepods were relatively tolerant to the compound but cladoceran populations were eliminated within 1–2 d. Interestingly enough, no deleterious effects were observed in rotifers.

Zooplankton possess various mechanisms that obviate interspecific competition (Hutchinson 1951); one of the most important is differential seasonal incidence of zooplankton species. The impact of permethrin on the inherent seasonal variation of the rotifer species complex may be discerned in part from Fig. 4. *Conochilus unicornis* first appears (day 42) in corrals exposed to permethrin and is more abundant in the treated corrals than in the controls. By day 42 the concentration of permethrin is <0.5% of the initial concentration, so toxicity is presumably not a factor at this time. It seems more probable that the appearance of *C. unicornis* can be attributed to the indirect impact of permethrin on seasonal succession of rotifer species. This effect is even more pronounced in the 5.0 than in the 0.5 µg permethrin $\cdot L^{-1}$ concentration.

Two types of numerical responses of zooplankton exposed to permethrin were observed: (1) direct numerical reduction due to acute toxicity of pesticide and (2) indirect numerical increase

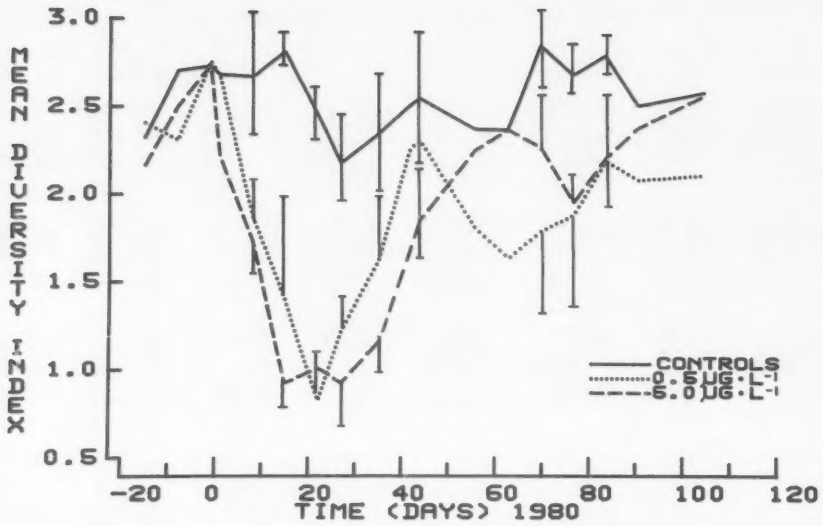


FIG. 5. Changes in diversity of zooplankton in response to the application of permethrin to limnocorrals in 1980.

which can be attributed to the release from predatory or competitive interactions as a result of (1). Diversity indices calculated separately for macrozooplankton and microzooplankton decrease regardless of the type of response. However, only diversity indices for the macrozooplankton in treated corrals were significantly lower ($P \leq 0.05$) than those in the controls; consequently, the overall impact of permethrin was to significantly lower the zooplankton diversity in the treated enclosures (Fig. 5).

The relatively large size of limnocorrals allows for some stability in predator–prey and competitive relationships. The impact of the pesticide on these interactions could not have been discerned from laboratory studies but has been elucidated using limnocorrals. The response of rotifers in corrals treated with permethrin represents such an interaction, and although differential toxicity could have been predicted from laboratory bioassays, confirmation of these findings could be made under conditions that would be difficult if not impossible to attain in the laboratory. These results thus testify to the potential of the limnocorral technique for use in ecotoxicological studies of pesticides.

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## References

ALLAN, J. D., AND C. E. GOULDEN. 1980. Some aspects of reproductive variation among freshwater zooplankton, p. 388–410. *In* W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. University Press of New England, London, England.

BANSE, K. 1982. Experimental marine ecosystem enclosures in a historical perspective, p. 11–24. *In* G. D. Grice and M. R. Reeve [ed.] Marine mesocosms: biological and chemical research in experimental ecosystems. Springer-Verlag, N.Y. Inc., New York, NY.

BRANDL, Z., AND C. H. FERNANDO. 1978. Prey selection by the cyclopoid copepods *Mesocyclops edax* and *Cyclops vicinus*. Verh. Int. Ver. Limnol. 20: 2505–2510.

BRANDLOVA, J., Z. BRANDL, AND C. H. FERNANDO. 1972. The cladocera of Ontario with remarks on some species and distribution. Can. J. Zool. 50: 1373–1403.

CAIRNS, J. 1983. Are single species toxicity tests alone adequate for estimating environmental hazard? Hydrobiologia 100: 45–57.

CHENGALATH, R., C. H. FERNANDO, AND M. G. GEORGE. 1971. The planktonic Rotifera of Ontario with keys to Genera and Species. Univ. Waterloo Fac. Environ. Stud. Occas. Pap., Waterloo, Ont. 41 p.

DORTLAND, R. J. 1980. Toxicological evaluation of parathion and aginphos-methyl in freshwater model ecosystems. Agric. Res. Rep. 898, ESBN 90 220 0732 4. 112 p.

EDMONDSON, W. T. 1959. Rotifera, p. 420–494. *In* W. T. Edmondson [ed.] Freshwater biology. John Wiley & Sons, Inc., New York, NY.

GROTHE, D. W., AND D. R. GROTHE. 1977. An illustrated key to the planktonic rotifers of the Laurentian Great Lakes. U.S. Environmental Protection Agency, Chicago, IL. 53 p.

HANEY, J. F., AND D. J. HALL. 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. Limnol. Oceanogr. 18: 331–333.

HODSON, P. V., AND E. S. MILLARD. 1978. Experimental ecosystems as a means of evaluating the fate and effects of contaminants in aquatic ecosystems. Proc. 4th Annu. Aquatic Toxicity Workshop, Vancouver, B.C., Nov. 8–10, 1977. Fish. Mar. Serv. Tech. Rep. 818: 211 p.

HUGHES, D. N., M. G. BOYER, M. H. PAPST, AND C. D. FOWLE. 1980. Persistence of three organophosphorus pesticides and some biological implications. Arch. Environ. Contam. Toxicol. 9: 269–279.

HURLBERT, S. 1975. Secondary effects of pesticides on aquatic ecosystems. Residue Rev. 57: 81–148.

HURLBERT, S. H., M. S. MULLA, AND H. R. WILSON. 1972. Effects of an organophosphorus insecticide on the phytoplankton, zooplankton, and insect populations of fresh-water ponds. Ecol. Monogr. 42: 289–299.

HUTCHINSON, G. E. 1951. Copepodology for the ornithologist. Ecology 32: 571–577.

JOLLY, A. L., J. W. AVAULT, K. L. KOONCE, AND J. B. GRAVES. 1978. Acute toxicity of permethrin to several aquatic animals. Trans. Am. Fish. Soc. 107: 825–827.

KINGSBURY, P. D. 1976. Studies of the impact of aerial applications of the synthetic pyrethroid NRDC-143 on aquatic ecosystems. Information Rep. CC-X-127, Environment Canada, Ottawa, Ont. 111 p.

MARSHALL, J. S., AND D. L. MELLINGER. 1980. Dynamics of cadmium-stressed plankton communities. Can. J. Fish. Aquat. Sci. 37: 403–414.

McLEESE, D. W., C. D. METCALFE, AND V. ZITKO. 1980. Lethality of permethrin, cypermethrin and fenvalerate to salmon, lobster, and shrimp. Bull. Environ. Contam. Toxical. 25: 950–955.

MIURA, T., AND R. M. TAKAHASHI. 1976. Effects of a synthetic pyrethroid, SD43775, on nontarget organisms when utilized as a mosquito larvicide. Mosq. News 36: 322–326.

MUIRHEAD-THOMSON, R. C. 1977. Lethal and behavioral impact of permethrin (NRDC-143) on selected stream macroinvertebrates. Mosq. News 38: 185–190.

NEILL, W. E. 1984. Regulation of rotifer densities by crustacean zooplankton in an oligotrophic montane lake in British Columia. Oecologia 61: 175–181.

PAPST, M. H., AND M. G. BOYER. 1980. Effects of two organophosphorus insecticides on the chlorophyll A and pheopigment concentrations of standing ponds. Hydrobiologia 69: 245–250.

PENNAK, R. W. 1978. Freshwater invertebrates of the United States. 2nd ed. John Wiley & Sons, Inc., New York, NY. 803 p.

PILSON, M. E. Q., AND S. NIXON. 1980. Marine microcosms in ecological research, p. 724–741. *In* J. P. Geisy [ed.] Microcosms in ecological research. Dep. Energy Symp. Ser. 52: 1110 p.

POOLE, R. W. 1974. An introduction to quantitative ecology. McGraw-Hill, Inc., New York, NY. 532 p.

SMIES, M. 1983. On the relevance of microecosystems for risk assessment: some considerations for environmental toxicology. Ecotoxicol. Environ. Saf. 5: 106–134.

SMITH, K., AND C. H. FERNANDO. 1978. A guide to the freshwater calanoid and cyclopoid copepoda crustacea of Ontario. Univ. Waterloo Fac. Environ. Stud. Occas. Pap., Waterloo, Ont. 74 p.

SOLOMON, K. R., J. Y. YOO, D. LEAN, N. K. KAUSHIK, K. E. DAY, AND G. L. STEPHENSON. 1985. Dissipation of permethrin in limnocorrals. Can. J. Fish. Aquat. Sci. 42: 70–76.

SOLOMON, K. R., K. SMITH, G. GUEST, J. Y. YOO, AND N. K. KAUSHIK. 1980. Use of limnocorrals in studying the effects of pesticides in the aquatic ecosystem. Can. Tech. Rep. Fish. Aquat. Sci. 975: 1–9.

SOLOMON, K. R., K. SMITH, AND G. L. STEPHENSON. 1982. Depth integrating samplers for use in limnocorrals. Hydrobiologia 94: 71–75.

STEELE, R. G. D., AND F. J. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, London, UK. 633 p.

STEPHENSON, R. R. 1982. Aquatic toxicology of cypermethrin: I. Acute toxicity to some freshwater fish and invertebrates in laboratory tests. Aquat. Toxicol. 2: 175–185.

URECH, J. 1979. Effects of increased heavy metal load in crustacea plankton. Schweiz. Z. Hydrol. 41: 247–260.

WARD, J. 1955. A description of a new zooplankton counter. Q. J. Microsc. Sci. 96: 371–373.

# Zinc–Phosphorus Interactions and Variation in Zinc Accumulation during Growth of *Chlamydomonas variabilis* (Chlorophyceae) in Batch Culture

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Bates, S. S., A. Tessier, P. G. C. Campbell, and M. Létourneau 1985. Zinc–phosphorus interactions and variation in zinc accumulation during growth of *Chlamydomonas variabilis* (Chlorophyceae) in batch culture. Can. J. Fish. Aquat. Sci. 42: 86–94.

Concentrations of EDTA-extractable zinc ($[Zn]_a$ ~ surface-bound zinc) and non-EDTA-extractable zinc ($[Zn]_c$ ~ transported zinc) were measured over the growth cycle of *Chlamydomonas variabilis* Dangeard growing in pH-controlled batch culture in the presence of six concentrations of free ionic zinc. Values of $[Zn]_a$ generally decreased throughout the growth cycle in batch culture, the exact pattern of change depending on whether the cells used to inoculate the experiment were obtained from a stock culture in the exponential or stationary growth phase. Concentrations of cellular TCA-insoluble phosphorus (polyphosphate) also declined throughout the growth cycle. Values of $[Zn]_c$ increased linearly throughout the exponential phase for growth at all zinc concentrations studied, but during the stationary phase they either reached a plateau for growth at 1.4 and 8.4 μmol $Zn^{2+} \cdot L^{-1}$, continued to increase linearly for growth at 13.2, 15.8, and 20.6 μmol $Zn^{2+} \cdot L^{-1}$, or declined for growth at 25.4 μmol $Zn^{2+} \cdot L^{-1}$. The cell yield of *C. variabilis* during the stationary phase was significantly decreased (by up to 90%) for growth in the presence of high concentrations of free ionic zinc. These cells also contained significantly more phosphorus than those grown in the presence of low free ionic zinc concentrations, but did not remove all of the initially added phosphorus from the growth medium. We hypothesize that cellular polyphosphate binds the transported zinc. As the concentration of cellular polyphosphate declines with increasing culture age, a portion of the previously bound intracellular zinc is released into the cell and exceeds a critical threshold, disrupting phosphorus metabolism, interfering with cell division, and decreasing cell yield.

Les concentrations de zinc extractible à l'EDTA ($[Zn]_a$ ~ zinc associé à la surface des cellules) et non extractible à l'EDTA ($[Zn]_c$ ~ zinc transporté) ont été mesurées au cours du cycle de croissance de *Chlamydomonas variabilis* Dangeard cultivée dans un milieu à pH-contrôlé en présence de six concentrations de zinc libre. Les valeurs de $[Zn]_a$ diminuaient généralement au cours du cycle de croissance ; la forme exacte du changement dépendait si les cellules utilisées pour l'inoculation provenaient d'une culture mère en phase de croissance exponentielle ou stationnaire. Les concentrations de phosphore cellulaire insoluble dans l'acide trichloroacétique (polyphosphate) diminuaient aussi au cours du cycle de croissance. Les valeurs de $[Zn]_c$ augmentaient linéairement au cours de la phase exponentielle de croissance pour toutes les concentrations de zinc étudiées mais, durant la phase stationnaire, elles atteignaient un plateau pour la croissance à 1,4 et 8,4 μmol $Zn^{2+} \cdot L^{-1}$, continuaient à croître linéairement pour la croissance à 13,2, 15,8 et 20,6 μmol $Zn^{2+} \cdot L^{-1}$, ou diminuaient pour la croissance à 25,4 μmol $Zn^{2+} \cdot L^{-1}$. La biomasse de *C. variabilis* obtenue pour la phase stationnaire diminuait (jusqu'à 90 %) lorsque l'algue était cultivée en présence de fortes concentrations de zinc libre. Ces cellules contenaient aussi, de façon significative, plus de phosphore que celles cultivées en présence de faibles concentrations de zinc libre, mais elles n'enlevaient pas tout le phosphore initialement ajouté dans le milieu de croissance. Nous suggérons que le polyphosphate cellulaire s'associe le zinc transporté dans la cellule. Lorsque la concentration de polyphosphates cellulaires diminue avec l'âge de la culture, une partie du zinc intracellulaire qui y était lié est relâché dans la cellule jusqu'à dépasser un niveau critique qui affecte le métabolisme du phosphore, interfère avec la division cellulaire et diminue la biomasse.

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The changing physiological state of phytoplankton during the different phases of growth in batch culture may influence the degree to which trace metals are bioaccumulated and/or become toxic. Exponentially growing cells generally accumulate metals more rapidly than do stationary phase cells (Saraiva and Fraizier 1975; De Filippis and Pallaghy 1976; Jennings and Rainbow 1979; Bates et al. 1983), although the opposite result has been noted (Cain et al. 1980). The apparent sensitivity of phytoplankton to a given total metal concentration also generally decreases with increasing culture age (Gibson 1972; Hutchinson and Stokes 1975; Laube et al. 1980).

Several possible explanations for these effects of culture age

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can be envisaged. Excretion of organic matter into the culture medium during the different stages of growth may play a role (McKnight and Morel 1979; Butler et al. 1980; Laube et al. 1980), as may loss of metals from the cells during the stationary phase (Hayward 1969; Davies 1973; 1974; Skaar et al. 1974; Cossa 1976; Schulz-Baldes and Lewin 1976; Butler et al. 1980; Laube et al. 1980). Alternatively, the changing chemical composition of the phytoplankton population during its growth cycle in batch culture (Healey 1973) may influence the degree to which trace metals are accumulated (Davies 1973; Skaar et al. 1974). Trace metals themselves may affect the chemical composition of phytoplankton cells at any time during the growth cycle by directly or indirectly interfering with nutrient uptake (Rana and Kumar 1974; Cloutier-Mantha and Harrison 1980; Rueter and Morel 1981; Rueter et al. 1981; Rueter 1983) or metabolism (Conway 1978).

We reported previously that both the concentration of EDTA-extractable zinc ($[Zn]_a$) and the flux ($F$) of zinc across the cell membrane decreased with increasing culture age for *Chlamydomonas variabilis* growing in pH-controlled batch culture in the presence of 7.0 μmol $Zn^{2+} \cdot L^{-1}$ (Bates et al. 1983). Our purpose here was to examine this phenomenon at several zinc concentrations and to investigate the possible role of zinc–phosphorus interactions in regulating cell division rates and final cell yields in batch culture.

## Materials and Methods

A stock culture of *Chlamydomonas variabilis* Dangeard, Chlorophyceae, strain 511/5 (ex-Centre de Recherche Hydrobiologique de Gif-sur-Yvette, France) was maintained for 16 mo in AAP medium (Payne 1975) without added zinc; the ionic species distribution in the normalAAP medium is given in Bates et al. (1982). Aliquots of the axenic stock culture, taken in the late stationary phase for experiment I and in the early exponential phase for experiment II, were inoculated into cylindrical vessels (New Brunswick Scientific Co., Inc.) containing 4 L of AAP medium. The batch cultures were grown at 20°C with an irradiance of approximately 150 $\mu E \cdot m^{-2} \cdot s^{-1}$ provided by a bank of cool white fluorescent lights with a 12 h light : 12 h dark photoperiod. Cultures were stirred with a Teflon-coated magnet and by bubbling with sterile air. The pH of the cultures was measured continuously and maintained at 7.0 ± 0.4 by automatic addition of $CO_2$; this addition was controlled with a model 5997-20 pH-controller (Horizon Ecology Co.) coupled to a model 885 automatic electrode switcher and a model 751 digital printer (Orion Research, Inc.).

Experiment I was designed to investigate changes in the concentrations of "adsorbed" and "transported" zinc during the batch culture growth of *C. variabilis* exposed to six different concentrations of free ionic zinc. The initial concentration of total zinc, containing trace quantities of carrier-free $^{65}Zn$ (New England Nuclear Corp.) to give a final radioactivity of approximately 0.6 MBq·$L^{-1}$, was 29.6 μmol·$L^{-1}$. Different concentrations of EDTA (4.2, 9.0, 13.8, 16.4, 21.2, and 28.2 μmol·$L^{-1}$) were added to achieve the desired initial concentrations of free ionic zinc ($[Zn^{2+}]$) in each culture vessel (Table 1). The solutions were allowed to equilibrate for approximately 20 h prior to inoculation with *C. variabilis*. A control vessel contained 0.81 μmol EDTA·$L^{-1}$ (equivalent to that found in the AAP medium) and no added zinc. Single aliquots were removed daily from the batch cultures between 09:00 and 11:30 to measure zinc adsorption and transport, as described below,

TABLE 1. Concentrations of total particulate phosphorus ($[P]_T$) and phosphorus removed from solution determined on day 8 (late stationary phase) for cultures of *C. variabilis* (experiment I) grown in six concentrations of computed initial free ionic zinc ($[Zn^{2+}]$). The initial concentration of phosphate added was 5.2 μmol·$L^{-1}$.

| Vessel No. | $[Zn^{2+}]$ (μmol·$L^{-1}$) | $[P]_T$ (μmol·$g^{-1}$) | P removed (%) |
|---|---|---|---|
| 1 | 1.4 | 31.7 | 96.2 |
| 2 | 8.4 | 30.9 | 88.7 |
| 3 | 13.2 | 36.1 | 77.1 |
| 4 | 15.8 | 41.3 | 61.0 |
| 5 | 20.6 | 44.3 | 64.0 |
| 6 | 25.4 | 257.9 | 22.0 |

over the growth cycle of *C. variabilis*. The concentration of $Zn^{2+}$ was calculated with a chemical equilibrium model (Bates et al. 1982). Addition of EDTA to the medium containing a constant zinc concentration alters the speciation of metals other than zinc. The calculated values for $[Cu^{2+}]$ and $[Fe^{3+}]$, for example, decrease from $2 \times 10^{-12}$ to $2 \times 10^{-14}$ mol·$L^{-1}$ and from $2 \times 10^{-15}$ to $8 \times 10^{-17}$ mol·$L^{-1}$, respectively, when the EDTA concentration is increased from 4.2 to 28.2 μmol·$L^{-1}$ in the AAP medium containing 29.6 μmol total Zn·$L^{-1}$.

For the zinc determinations, each aliquot (40 mL) was centrifuged for 10 min at approximately 500 × $g$ in polycarbonate centrifuge tubes. The supernatant was removed for determination of $^{65}Zn$ radioactivity and provided a measure of the concentration of zinc remaining in the bulk solution after incubation with the algae, $[Zn]_b$. The pellet was then resuspended in 10.0 mL of a solution (pH 7.0) containing $10^{-4}$ mol EDTA·$L^{-1}$ plus $6 \times 10^{-4}$ mol $CaCl_2 \cdot L^{-1}$ (added to adjust the ionic strength) in darkness for 10 min. After centrifugation (10 min), the supernatant was removed for determination of $^{65}Zn$ radioactivity and provided an estimate of the concentration of zinc previously adsorbed onto the cell surface, $[Zn]_a$. This concentration is operationally defined as the concentration of zinc extracted by the EDTA (Bates et al. 1982). The pellet was then transferred to a test tube with 5.0 mL of deionized water for determination of $^{65}Zn$ radioactivity, to provide a measure of the concentration of zinc transported across the cell membrane, $[Zn]_c$. This concentration is operationally defined as the concentration of zinc remaining within the cells after extraction with EDTA (Bates et al. 1982). The total zinc concentration, $[Zn]_T$, calculated from the mass balance equation $[Zn]_T = [Zn]_b + [Zn]_a + [Zn]_c$, generally agreed within a few percent with the added zinc concentration. The effects of centrifugation and of EDTA extraction on zinc accumulation by *C. variabilis* were minimal (Bates et al. 1982).

Experiment II was designed to investigate the relationship between zinc uptake and cellular phosphorus measured daily over the growth cycle of *C. variabilis* in batch culture. In this experiment, the initial concentrations of total nonradioactive zinc were 0, 2.4, and 11.1 μmol·$L^{-1}$, giving calculated free ionic zinc concentrations of 0, 1.9, and 10.4 μmol·$L^{-1}$, respectively, in the three vessels used; the initial concentrations of EDTA (0.81 μmol·$L^{-1}$) and of phosphorus (6 μmol·$L^{-1}$), as well as of all the other elements, remained the same as in the AAP medium (Bates et al. 1982). The calculated values for $[Cu^{2+}]$ and $[Fe^{3+}]$ increased from $5 \times 10^{-14}$ to $4 \times 10^{-12}$ mol·$L^{-1}$ and from $2 \times 10^{-16}$ to $3 \times 10^{-15}$ mol·$L^{-1}$ respectively, when $[Zn^{2+}]$ was increased to 10.4 μmol·$L^{-1}$. After

overnight equilibration of the autoclaved media, trace quantities of carrier-free [$^{32}$P]phosphate (New England Nuclear Corp.) were added to give a final radioactivity in solution of 0.3 Bq·L$^{-1}$. The media were then inoculated with *C. variabilis* obtained from a stock culture in early exponential growth phase. The initial cell concentration in this experiment ($1.2 \times 10^5$ cells·mL$^{-1}$) was higher than that used in experiment I ($9.1 \times 10^3$ cells·mL$^{-1}$) to allow measurement on day 0, immediately after addition of zinc. Triplicate daily aliquots were taken from each batch culture to determine $[Zn]_b$, $[Zn]_a$, and $[Zn]_c$, as described above.

On the last day of experiment I (day 8), total particulate phosphorus was determined on 20- to 155-mL culture aliquots by filtration through washed glass fiber filters (type A/E, Gelman Instrument Co.) according to the method of Stainton et al. (1974). Cellular polyphosphate was determined daily in experiment II according to the procedure of Elgavish and Elgavish (1980). Each aliquot (40 mL) was centrifuged for 10 min at approximately 500 × *g*, and the pellet was extracted for 30 min at 0°C in darkness with 10 mL of ice-cold 6% (w/v) trichloroacetic acid (TCA). The samples were then centrifuged (10 min) and the supernatant was removed for determination of $^{32}$P radioactivity in the TCA-soluble fraction. The pellet was transferred to a scintillation vial with 5.0 mL of deionized water for determination of $^{32}$P radioactivity in the TCA-insoluble fraction.

Chlorophyll *a* (Chl *a*) was determined by mixing a 0.5-mL sample of culture material with 4.5 mL of absolute acetone and measuring the fluorescence immediately with a fluorometer (Turner Designs, model 10-005 R) calibrated with pure Chl *a* (Sigma Chemical Co.). In a control experiment, direct extractions of the culture aliquots with acetone gave similar results to Chl *a* measured in acetone extracts of cells collected on a glass fiber filter. However, the presence of dissolved zinc at the concentrations we used diminished the fluorescence value by 15–20%.

Radioactivity of $^{65}$Zn was determined with a model 3380 Tri-Carb liquid scintillation spectrophotometer coupled to a model 5022 Auto-gamma spectrometer (Packard Instrument Co., Inc.). Radioactivity of $^{32}$P was determined by Cerenkov radiation using a model 1215 Rackbeta liquid scintillation counter (LKB Wallac). Stable zinc was analyzed by flame atomic absorption spectrophotometry (Varian Techtron model AA-575 ABQ). Cell numbers were determined daily in each culture with a model $T_A$ Coulter counter. Cell dry weights were determined daily with an electrobalance (Mettler model ME30) after filtration of 10–50 mL of culture onto preweighed Nuclepore filters (1.0 μm, 25-mm diameter) and drying at 75°C to constant weight.

## Results

The division rate of *C. variabilis* in experiment I was only slightly reduced by the presence of free ionic zinc at initial concentrations of up to 13.2 μmol·L$^{-1}$ (Fig. 1). These results are in agreement with those of our previous study conducted with batch cultures growing with a 12 h light : 12 h dark photoperiod (Bates et al. 1982). However, these findings differ from those of a study conducted with batch cultures growing with continuous light in which the division rate was decreased by approximately 30% in the presence of 7 μmol $Zn^{2+}$·L$^{-1}$ (Bates et al. 1983). Cadmium, for example, is also more toxic to the chlorophyte *Coelastrum proboscideum* in continuous light

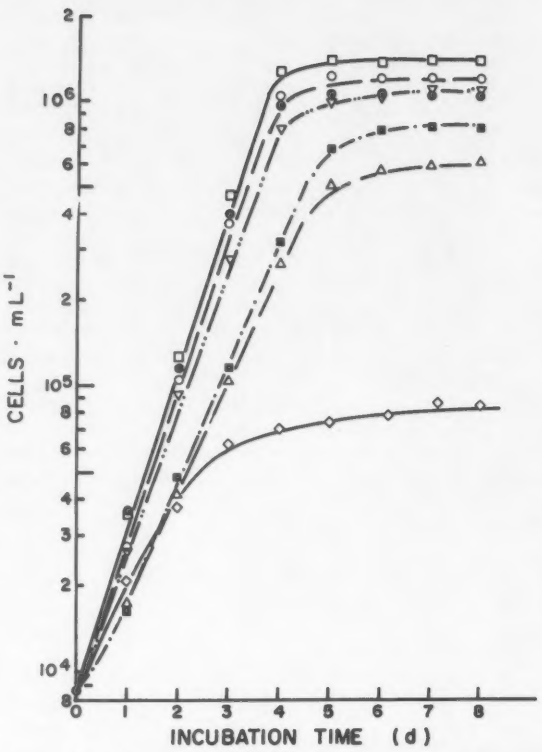


FIG. 1. Growth curves of *C. variabilis* (experiment I) in the presence of various concentrations (μmol $Zn^{2+}$·L$^{-1}$) of computed initial free ionic zinc (●, 0; □, 1.4; ○, 8.4; ▽, 13.2; ■, 15.8; △, 20.6; ◇, 25.4).

than when a light:dark photoperiod is used (Hornung et al. 1981). By comparison, the division rate of the freshwater chlorophyte *Scenedesmus quadricauda* was reduced by 50% in the presence of 7.9 μmol $Zn^{2+}$·L$^{-1}$ in continuous light (Petersen 1982). The biomass achieved during the stationary phase in experiment I was significantly decreased at the higher zinc concentrations, whether the data were expressed as cell numbers or as cellular dry weight (Fig. 1), in agreement with Bates et al. (1983).

Average cellular dry weight decreased during the exponential growth phase for experiment I, and then increased during the stationary phase (Fig. 2a). Such an increase is normally attributed to an uncoupling of photosynthesis from cell division as a normal consequence of nutrient deficiency in batch culture (Healey 1973). The dry weight of cells growing with zinc was greater than that of the control, suggesting a further uncoupling of cytokinesis from other metabolic processes (Davies 1974; Rivkin 1979). An exception to this was the culture grown at the highest zinc concentration (25.4 μmol·L$^{-1}$), in which microscopic observation indicated a large proportion of lysed cells. The increase in dry weight due to metal exposure is often attributed to an inhibition of excretion of carbon compounds (De Filippis and Pallaghy 1976; Li 1979; Fisher et al. 1981). However, other studies indicate that organic matter may be excreted in the presence of metals, whether measured directly (McKnight and Morel 1979; Butler et al. 1980) or inferred (Rivkin 1979; Laube et al. 1980).

Cellular Chl *a* content decreased with increasing culture age

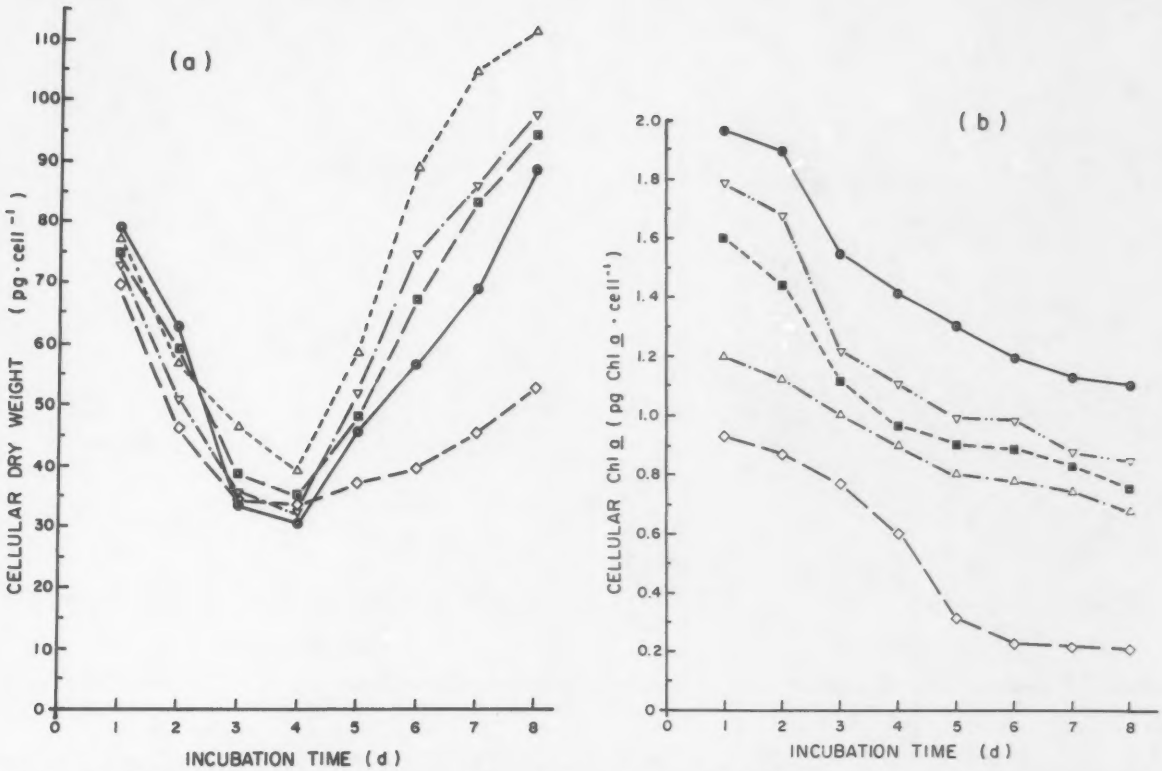


FIG. 2. (a) Cellular dry weight and (b) Chl *a* content of *C. variabilis* as a function of the incubation time with several concentrations (μmol $Zn^{2+} \cdot L^{-1}$) of computed free ionic zinc (experiment I) (●, 0; ▽, 13.2; ■, 15.8; △, 20.6; ◇, 25.4). Data for 1.4 and 8.4 μmol $Zn^{2+} \cdot L^{-1}$ follow the same pattern as the other zinc concentrations but are omitted for clarity.

at about the same rate whether the cells were grown in the presence or absence of added zinc (Fig. 2b), presumably as a normal consequence of nutrient deficiency in batch culture (Healey 1973). However, cells grown with zinc contained less Chl *a* than did those of the control, the effect being more pronounced at the high zinc concentrations; this effect cannot be explained completely by the 15–20% reduction in Chl *a* fluorescence in the presence of zinc. Li and Ueng (1982) observed that ionic zinc lowered the Chl *a* fluorescence of isolated oat chloroplasts, and suggested that it affects the fluorescence quenching properties of the reaction centers of photosystem II. A similar decrease in cellular Chl *a* in the presence of metals has been observed by others (e.g. Conway 1978) and was attributed to the inhibition by the metal of the reductive steps leading to the biosynthesis of this pigment (De Filippis et al. 1981).

The concentration of total particulate phosphorus was determined on day 8 during the stationary phase in experiment I. Cells exposed to the highest zinc concentrations contained more total particulate phosphorus, and took up less phosphorus from the solution than did cells grown at low zinc concentrations (Table 1). Similar results were obtained in experiment II.

Changes in the concentrations of zinc bound to cell surfaces, $[Zn]_a$, and transported into the cells, $[Zn]_c$, during growth of the test populations in experiment I are shown in Fig. 3. Values of $[Zn]_a$ reached a peak during the mid-exponential growth phase, and then decreased during the late exponential phase to attain a low, stable value during the late stationary phase (Fig. 3a). The cell biomass was too low to obtain an accurate measure of $[Zn]_a$ on day 1. Values of $[Zn]_c$ increased linearly during the exponential growth phase, and then reached a plateau for growth in the presence of ionic zinc concentrations of 1.4 and 8.4 μmol·$L^{-1}$ (Fig. 3b). For growth in the presence of 13.2, 15.9, and 20.6 μmol $Zn^{2+} \cdot L^{-1}$, however, $[Zn]_c$ increased linearly during the entire 8-d incubation period. For growth in the presence of 25.4 μmol $Zn^{2+} \cdot L^{-1}$, $[Zn]_c$ increased only during the exponential growth phase, and then decreased during the stationary phase when a large proportion of cellular debris was also found.

Changes in cell number, percentage of phosphorus taken up by the cells, and TCA-soluble and TCA-insoluble phosphorus as a function of culture age and initial concentration of free ionic zinc for experiment II are shown in Fig. 4. Most of the added $^{32}P$ was taken up by the cells within the first day, presumably within the first 2–3 h; the level of phosphorus in solution then remained the same for several days. If the values obtained during this plateau are considered (days 1–7), the mean value of phosphorus removed from solution at the highest concentration of ionic zinc ($[Zn^{2+}] = 10.4$ μmol·$L^{-1}$) is statistically different ($P < 0.001$; Student *t*-test) from the other two mean values of total phosphorus removed (for $[Zn^{2+}] = 0$ or 1.4 μmol·$L^{-1}$). Although phosphorus uptake was rapid, exponential division started only after a lag phase of about 1 d. The cellular phosphorus was largely found in the TCA-insoluble fraction, presumably as polyphosphate-phosphorus (Elgavish and Elgavish 1980). Concentrations of both TCA-soluble and TCA-

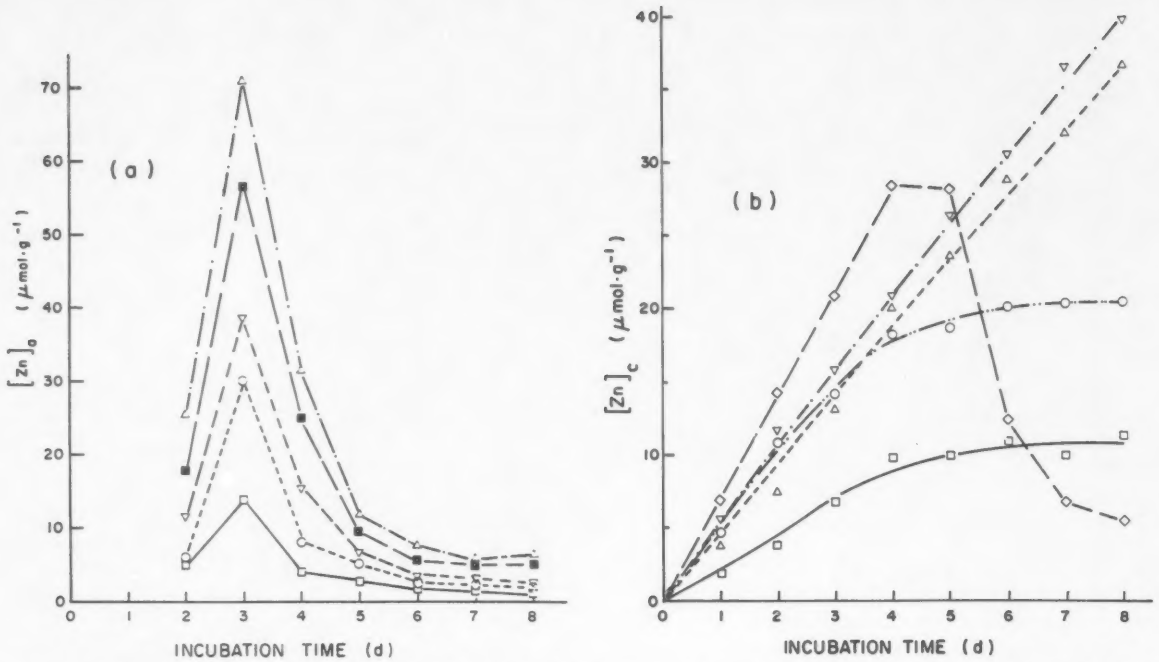


FIG. 3. Concentrations of (a) EDTA-extractable and (b) transported zinc (experiment I), normalized to cell dry weight, for *C. variabilis* as a function of incubation time with several concentrations ($\mu$mol $Zn^{2+}\cdot L^{-1}$) of computed ionic zinc (□, 1.4; ○, 8.4; ▽, 13.2; ■, 15.8; △, 20.6; ◇, 25.4).

insoluble phosphorus decreased exponentially with culture age, as the cells divided and metabolized the phosphorus pools. A comparison of Fig. 4a, 4b, and 4c indicates that the presence of zinc led to an appreciable decrease (~20%) in the cell yield, a slight decrease in the division rate, an accumulation of cellular phosphorus, and to an increased proportion of phosphorus remaining in the growth medium. These effects became more apparent as the initial free ionic zinc concentration, $[Zn^{2+}]_b$, increased from 1.9 to 10.4 $\mu$mol·$L^{-1}$.

Changes in $[Zn]_b$ with time, along with changes in $[Zn]_a$ and $[Zn]_c$, normalized to culture volume, are shown in Fig. 5 for the culture grown at an initial free ionic zinc concentration of 10.4 $\mu$mol·$L^{-1}$. The decrease in $[Zn]_b$ with incubation time was due primarily to an increase in the non-EDTA-extractable zinc fraction rather than to the EDTA-extractable zinc fraction. The same pattern was observed for the culture grown at an initial free zinc concentration of 1.9 $\mu$mol·$L^{-1}$, and for experiment I.

As in experiment I (Fig. 3a), values of $[Zn]_a$, normalized to cellular dry weight, decreased with culture age to attain a low, stable value during the late stationary phase (Fig. 6); this pattern parallels that found for cellular TCA-soluble and TCA-insoluble phosphorus during the growth cycle (Fig. 4). However, in contrast with experiment I, a peak in $[Zn]_a$ was not seen during the late exponential growth phase; rather, values of $[Zn]_a$ declined continually from day 0 onward. Consistent with the results of experiment I (Fig. 3b), values of $[Zn]_c$ increased with time and tended toward a constant value during the stationary phase in the culture grown in the presence of 1.9 $\mu$mol $Zn^{2+}\cdot L^{-1}$, but continued to increase in the culture grown with 10.4 $\mu$mol $Zn^{2+}\cdot L^{-1}$ (Fig. 6).

## Discussion

In this study the concentration of free ionic zinc, $[Zn^{2+}]_b$, was varied purposefully, and various biological variables were monitored. Before attributing the biological response to changes in $[Zn^{2+}]_b$, however, one must first consider carefully the speciation changes undergone by other metals present in the culture medium. For example, varying $[Zn^{2+}]_b$, in the AAP medium, either by changing the EDTA concentration at constant $[Zn]_T$ or by varying $[Zn]_T$ at constant EDTA concentration, alters the free ion concentrations of copper and iron; for all experiments reported here, calculated values of $[Cu^{2+}]$ fall in the range of $10^{-14}$ to $10^{-12}$ mol·$L^{-1}$; values for $[Fe^{3+}]$ range from $8 \times 10^{-17}$ to $3 \times 10^{-15}$ mol·$L^{-1}$. Possibly, therefore, some of the toxic effects observed (e.g. inhibition of growth rate or decreased cell yield) could be due to interactions of the studied alga with trace metals other than zinc; possibilities to consider would include copper deficiency or toxicity and iron deficiency.

Copper deficiency has been reported for *Chlorella vulgaris* and *Oocystis marssonii* at $[Cu^{2+}] < 10^{-16}$ mol·$L^{-1}$ (Manahan and Smith 1973). Toxic effects of copper, on the other hand, are generally reported in the $[Cu^{2+}]$ range of $10^{-10}$ to $10^{-9}$ mol·$L^{-1}$; for a few sensitive algal strains, values for $[Cu^{2+}]$ as low as $10^{-11}$ mol·$L^{-1}$ have been suggested to be deleterious (Sunda and Guillard 1976; Anderson and Morel 1978; Gavis et al. 1981; Petersen 1982). Our calculated values of $[Cu^{2+}]$ clearly do not fall in the concentration ranges known to produce either deficiency or toxicity.

The onset of iron deficiency in *Thalassiosira weissflogii*

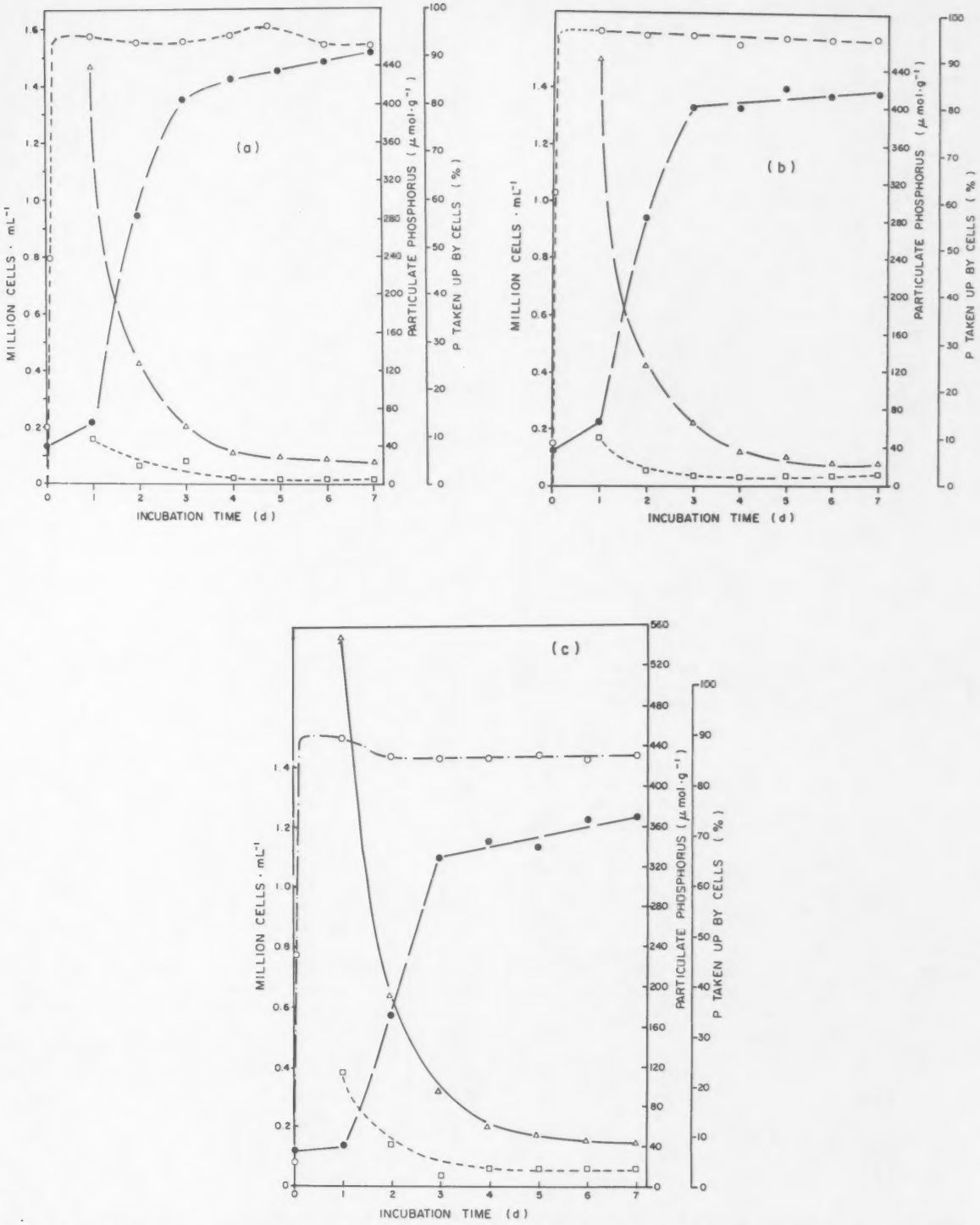


FIG. 4. Cell number (●), percentage of phosphorus removed from solution (○), and TCA-soluble (□) and TCA-insoluble (△) phosphorus concentrations (experiment II) as a function of incubation time for *C. variabilis* grown in (a) the absence of added zinc or (b) in the presence of 1.4 and (c) 10.4 μmol $Zn^{2+} \cdot L^{-1}$.

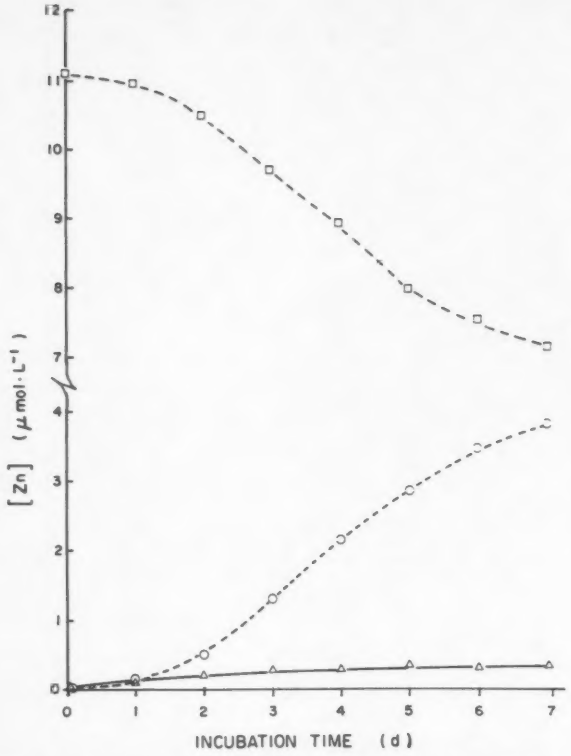


FIG. 5. Concentrations of EDTA-extractable zinc (△), transported zinc (○), and total zinc remaining in solution (□) (experiment II), normalized to culture volume, for *C. variabilis* growing in the presence of 10.4 μmol $Zn^{2+}\cdot L^{-1}$.

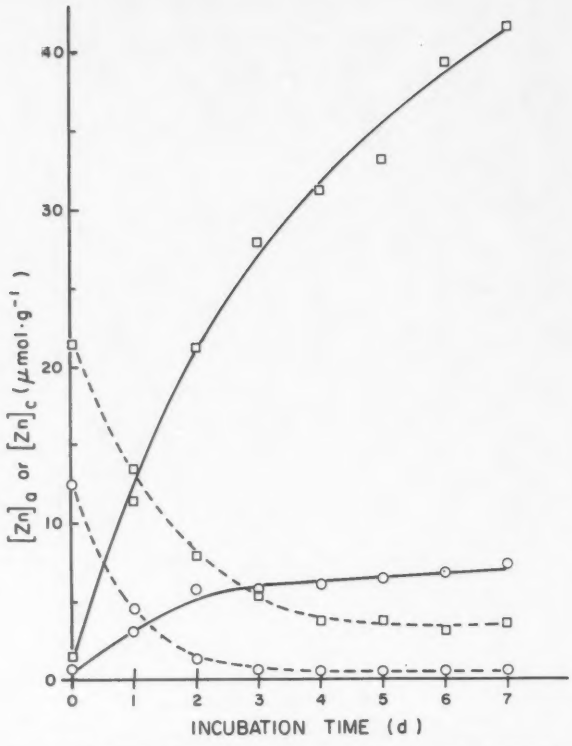


FIG. 6. Concentrations of EDTA-extractable (---) and transported (—) zinc (experiment II) as a function of incubation time in the presence of 1.9 (○) and 10.4 (□) μmol $Zn^{2+}\cdot L^{-1}$.

occurs at $[Fe^{3+}] = 10^{-19.9}$ mol·$L^{-1}$ (Anderson and Morel 1982), i.e. at levels that are still approximately $10^3$ times lower than our lowest calculated free iron concentration. However, the possibility of a zinc-induced limitation of iron uptake must also be considered. In effect, the uptake of iron by *T. weissflogii* has been shown to involve a membrane site with a high affinity for $Fe^{3+}$ (Anderson and Morel 1982). The possible competition of zinc with iron for the iron uptake sites must be examined in view of the high ratios ($\sim 10^{10}$) calculated for $[Zn^{2+}]/[Fe^{3+}]$ for our experiments; such an inhibition or iron uptake and assimilation by cadmium has been recently reported (Harrison and Morel 1983). One would, however, expect that any inhibition of cell division due to an iron deficiency induced by zinc would increase with increasing ratios $[Zn^{2+}]/[Fe^{3+}]$. In experiment I (but not II) we observe the contrary; inhibition of cell division increases with $[Zn^{2+}]$, and the calculated ratio $[Zn^{2+}]/[Fe^{3+}]$ decreases from $2.5 \times 10^{10}$ to $0.8 \times 10^{10}$ as $[Zn^{2+}]$ is increased from 1.4 to 25.4 μmol·$L^{-1}$.

As there is no evidence to suggest that the effects we observed on cell division are due to trace metals other than zinc, possible interactions between high free zinc concentrations and phosphorus metabolism are examined. Using results from experiments I and II, we hypothesize that during the early stages of growth (days 0–3), the TCA-insoluble (polyphosphate) phosphorus traps and thereby detoxifies the intracellular zinc at the lower free zinc concentrations (e.g. $[Zn^{2+}] < 10$ μmol·$L^{-1}$); cell division thus proceeds normally (Fig. 1, 4). However, as cell division continues, the cellular content of TCA-insoluble phosphorus declines due to the mobilization of polyphosphates for cell growth. This decline could release previously bound intracellular zinc, as well as prevent the detoxification of any subsequently transported zinc. As $[Zn]_c$ continues to increase (Fig. 3b), levels of unbound intracellular zinc could become toxic and interfere with cell division. For higher free zinc concentrations (e.g. $[Zn^{2+}] > 10$ μmol·$L^{-1}$), the inhibitory effect of zinc on cell division occurs earlier during the growth cycle, i.e. it affects the division rate during the exponential growth phase (e.g. compare Fig. 4a and 4c). Polyphosphate bodies are known to accumulate zinc (Jensen et al. 1982), and they apparently increase in number or size under conditions of metal stress, both in the laboratory (Jensen et al. 1982) and under natural conditions (Stoermer et al. 1981). Jensen et al. (1982) suggested that they act as storage sites for trace metals at low metal concentrations, and as detoxification sites when trace metals are at toxic levels. The relatively higher concentration of TCA-insoluble (polyphosphate) phosphate observed in the culture exposed to 10.4 μmol·$L^{-1}$ (Fig. 4c), compared with 0 and 1.2 μmol $Zn^{2+}\cdot L^{-1}$ (Fig. 4a, 4b), tends to support this.

The large decrease in $[Zn]_a$ with increasing culture age (Fig. 3a, 6), reported previously (Bates et al. 1983), could be due to at least two possible factors: (1) a decrease in $[Zn^{2+}]_b$ with which $[Zn]_a$ is presumably in equilibrium and/or (2) a change in the physicochemical characteristics of the cell surface as the culture ages. The concentration of dissolved zinc does decrease due to its removal from solution by the cells or cellular

debris (Fig. 5), but this decrease (~35%) is small compared with the decrease (~86%) in $[Zn]_a$ (Fig. 3a, 6). Furthermore, it is unlikely that excreted organic matter would reduce $[Zn^{2+}]_b$ sufficiently to explain the 10-fold decrease in $[Zn]_a$; a preliminary study where $[Zn^{2+}]_b$ was measured with an amalgam electrode (Zn/Hg) suggested that the organic matter excreted by *C. variabilis* grown in the AAP medium for approximately 40 h had only a minor complexation capacity for zinc (J. Buffle, Université de Genève, pers. comm.). We therefore favor the second possible factor, i.e. that the surface of the cell changes during growth in batch culture. These changes are consistent with those occurring during growth in the presence or absence of added zinc, where the cells' ability to adsorb zinc during a 10-min. incubation period also decreased with culture age (Bates et al. 1983).

Results of a previous study (Bates et al. 1983) indicated that the surface characteristics of *C. variabilis* are such that use of stationary phase cells leads to low values of $[Zn]_a$ during short-term incubations, whereas use of exponentially growing cells leads to high values of $[Zn]_a$. This too is consistent with our present results. Cells used to inoculate the batch cultures of experiment I were obtained from a stock culture in the late stationary phase; this may explain why values of $[Zn]_a$ were initially low and peaked on day 3 before decreasing again during the stationary phase (Fig 3a). In contrast, exponentially growing cells were used to inoculate experiment II; high values of $[Zn]_a$ were obtained early in the experiment after addition of zinc (Fig. 6).

In batch cultures, the cellular content of metals decreases with increasing culture age (Hayward 1969; Cossa 1976; Butler et al. 1980; Laube et al. 1980). However, a distinction has not been made, with the exception of Davies (1973), as to whether this decrease reflects changes in the adsorbed or the transported metal fractions. In the case of Davies (1973), the decrease with culture age in the total concentration of accumulated zinc was due to a decrease in transported zinc, presumably caused by a reduction in the pool of intracellular protein capable of binding the zinc. In our study, the manner in which $[Zn]_c$ changed with culture age is a function of the zinc concentration in which the cells were grown. At the lower ionic zinc concentrations (1.4, 1.9, and 8.4 $\mu mol \cdot L^{-1}$), we suggest that the plateau during the stationary phase (Fig. 3b, 6) reflects a steady-state situation (zinc transport into cell = zinc loss from cell + dilution due to residual growth), or that transport was related to cell physiology. However, zinc transport does not appear to be strongly related to cell physiology for growth in the presence of 13.2, 15.8, and 20.6 $\mu mol\ Zn^{2+} \cdot L^{-1}$ (Fig. 3b); under these latter conditions the net rate of zinc accumulation is unaffected by the passage from the exponential to the stationary phases. The culture grown at 10.4 $\mu mol\ Zn^{2+} \cdot L^{-1}$ (Fig. 6) showed an intermediate response (i.e. a curvilinear pattern). At the highest ionic zinc concentration (25.4 $\mu mol \cdot L^{-1}$), microscopic observation indicated that cell integrity was affected after about day 4; cellular dry weight (Fig. 2a) and Chl *a* (Fig 2b) were lower than for any other culture. These observations could explain the rapid decrease in $[Zn]_c$ during the stationary phase for the culture grown at 25.4 $\mu mol\ Zn^{2+} \cdot L^{-1}$ (Fig. 3b).

We conclude that the distinction between the concentrations of adsorbed and transported zinc, although operationally defined, provides information about the influence of cellular physiological state on the bioavailability and toxicity of trace metals. Evidence that the physicochemical characteristics of the phytoplankton cell surface change during the growth cycle of *C. variabilis* in batch culture was provided by monitoring zinc adsorption during growth in the presence of several concentrations of zinc (Bates et al. 1983). The measurement of specific cellular functions, e.g. phosphorus metabolism, suggested a possible role of macronutrients in regulating trace metal toxicity in phytoplankton.

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## References

ANDERSON, D. M., AND F. M. M. MOREL. 1978. Copper sensitivity of *Gonyaulax tamarensis*. Limnol. Oceanogr. 23: 283–295.

1982. The influence of aqueous iron chemistry on uptake of iron by the coastal diatom *Thalassiosira weissflogii*. Limnol. Oceanogr. 27: 789–813.

BATES, S. S., M. LÉTOURNEAU, A. TESSIER, AND P. G. C. CAMPBELL. 1983. Variation in zinc adsorption and transport during growth of *Chlamydomonas variabilis* (Chlorophyceae) in batch culture with daily addition of zinc. Can. J. Fish. Aquat. Sci. 40: 895–904.

BATES, S. S., A. TESSIER, P. G. C. CAMPBELL, AND J. BUFFLE.1982. Zinc adsorption and transport by *Chlamydomonas variabilis* and *Scenedesmus subspicatus* (Chlorophycea) grown in semicontinuous culture. J. Phycol. 18: 521–529.

BUTLER, M., A. E. J. HASKEW, AND M. M. YOUNG. 1980. Copper tolerance in the green alga, *Chlorella vulgaris*. Plant Cell Environ. 3: 119–126.

CAIN, J. R., D. C. PASCHAL, AND C. M. HAYDEN. 1980. Toxicity and bioaccumulation of cadmium in the colonial green algae *Scenesdesmus obliquus*. Arch. Environ. Contam. Toxicol. 9: 9–16.

CLOUTIER-MANTHA, L., AND P. J. HARRISON. 1980. Effects of sublethal concentrations of mercuric chloride on ammonium-limited *Skeletonema costatum*. Mar. Biol. 5: 219–231.

CONWAY, H. L. 1978. Sorption of arsenic and cadmium and their effects on growth, micronutrient utilization, and photosynthetic pigment composition of *Asterionella formosa*. J. Fish. Res. Board Can. 35: 286–294.

COSSA, D. 1976. Sorption du cadmium par une population de la diatomée *Phaeodactylum tricornutum* en culture. Mar. Biol. 34: 163–167.

DAVIES, A. G. 1973. The kinetics of and a preliminary model for the uptake of radio-zinc by *Phaeodactylum tricornutum* in culture, p. 403–420. *In* Radioactive contamination of the marine environment. International Atomic Energy Agency, Vienna.

1974. The growth kinetics of *Isochrysis galbana* in cultures containing sublethal concentrations of mercuric chloride. J. Mar. Biol. Assoc. U.K. 54: 157–169.

DE FILIPPIS, L. F., R. HAMPP, AND H. ZIEGLER. 1981. The effects of sublethal concentrations of zinc, mercury and cadmium on *Euglena*. Growth and pigments. Z. Planzenphysiol. 101: 37–47.

DE FILIPPIS, L. F., AND C. K. PALLAGHY. 1976. The effect of sub-lethal concentrations of mercury and zinc on *Chlorella*. I. Growth characteristics and uptake of metals. Z. Planzenphysiol. 78: 197–207.

ELGAVISH, A., AND G. A. ELGAVISH. 1980. $^{31}$P-NMR differentiation between intracellular phosphate pools in *Cosmarium* (Chlorophyta). J. Phycol. 16: 368–374.

FISHER, N. S., G. L. JONES, AND D. M. NELSON. 1981. Effects of copper and zinc on growth, morphology and metabolism of *Asterionella japonica* (Cleve). J. Exp. Mar. Biol. Ecol. 51: 37–56.

GAVIS, J., R. L. GUILLARD, AND B. L. WOODWARD. 1981. Cupric ion activity and the growth of phytoplankton clones isolated from different marine environments. J. Mar. Res. 39: 315–333.

GIBSON, C.E. 1972. The algicidal effect of copper on a green and blue-green alga and some ecological implications. J. Appl. Ecol. 9: 513–518.

HARRISON, G. I., AND F. M. M. MOREL. 1983. Antagonism between cadmium and iron in the marine diatom *Thalassiosira weissflogii*. J. Phycol. 19: 495–507.

HAYWARD, J. 1969. Studies on the growth of *Phaeodactylum tricornutum*. V. The relationship to iron, manganese and zinc. J. Mar. Biol. Assoc. U.K. 49: 439–446.

HEALEY, F. P. 1973. Inorganic nutrient uptake and deficiency in algae. Crit. Rev. Microbiol. 3: 69–113.

HORNUNG, U., H. VON WITSCH, AND F. MENKE. 1981. Cadmium repression of the growth of *Coelastrum proboscideum* Bohlin (Chlorococcales) and some counteracting factors. Arch. Hydrobiol. Suppl. 60 (Algol. Stud. 28): 298–312.

HUTCHINSON, T. C., AND P. M. STOKES. 1975. Heavy metal toxicity and algal bioassays, p. 320–343. Spec. Tech. Publ. 573. American Society for Testing and Materials, Philadelphia, PA.

JENNINGS, J. R., AND P. S. RAINBOW. 1979. Accumulation of cadmium by *Dunialla tertiolecta* Butcher. J. Plankton Res. 1: 67–74.

JENSEN, T. E., M. BAXTER, J. W. RACHLIN, AND V. JANI. 1982. Uptake of heavy metals by *Plectonema boryanum* (Cyanophyceae) into cellular components, especially polyphosphate bodies: an X-ray energy dispersive study. Environ. Pollut. Ser. A 27: 119–127.

LAUBE, V. M., C. N. MCKENZIE, AND D. J. KUSHNER. 1980. Strategies of response to copper, cadmium, and lead by a blue-green and a green alga. Can. J. Microbiol. 26: 1300–1311.

LI, W. K. W. 1979. Cellular composition and physiological characteristics of the diatom *Thalassiosira weissflogii* adapted to cadmium stress. Mar. Biol. 55: 171–180

LI, Y.-S., AND S.-H. UENG. 1982. Zinc or silicotungstate affects steady state chlorophyll *a* fluorescence of chloroplasts suspended in distilled water. Bot. Bull. Acad. Sin. (Taipei) 23: 27–38.

MANAHAN, S. E., AND M. J. SMITH. 1973. Copper micronutrient requirement for algae. Environ. Sci. Technol. 7: 829–833.

MCKNIGHT, D. M., AND F. M. M. MOREL. 1979. Release of weak and strong copper-complexing by algae. Limnol. Oceanogr. 24: 823–837.

PAYNE, A. G. 1975. Responses of the three test algae of the algal assay procedure: bottle test. Water Res. 9: 437–445.

PETERSEN, R. 1982. Influence of copper and zinc on the growth of a freshwater alga, *Scenedesmus quadricauda*: the significance of chemical speciation. Environ. Sci. Technol. 16: 443–447.

RANA, B. C., AND H. D. KUMAR. 1974. The toxicity of zinc to *Chlorella vulgaris* and *Plectonema boryanum* and its protection by phosphate. Phykos 13: 60–66.

RIVKIN, R. B. 1979. Effects of lead on growth of the marine diatom *Skeletonema costatum*. Mar. Biol. 50: 239–247.

RUETER, J. G. JR. 1983. Effect of copper on growth, silicic acid uptake and soluble pools of silicic acid in the marine diatom, *Thalassiosira weissflogii* (Bacillariophyceae). J. Phycol. 19: 101–104.

RUETER, J. G. JR., S. W. CHISHOLM, AND F. M. M. MOREL. 1981. Effects of copper toxicity on silicic acid uptake and growth in *Thalassiosira pseudonana*. J. Phycol. 17: 270–278.

RUETER, J. G. JR., AND F. M. M. MOREL. 1981. The interaction between zinc deficiency and copper toxicity as it affects the silicic acid uptake mechanisms in *Thalassiosira pseudonana*. Limnol. Oceanogr. 26: 67–73.

SARAIVA, M. C., AND A. FRAIZIER. 1975. Contamination par le $^{51}$Cr et le $^{109}$Cd de cultures de l'algue *Dunaliella bioculata*. Mar. Biol. 29: 343–350.

SCHULZ-BALDES, M., AND R. A. LEWIN. 1976. Lead uptake in two marine phytoplankton organisms. Biol. Bull. 150: 118–127.

SKAAR, H., B. RYSTAD, AND A. JENSEN. 1974. The uptake of $^{63}$Ni by the diatom *Phaeodactylum tricornutum*. Physiol. Plant. 32: 353–358.

STAINTON, M. R., M. J. CAPEL, AND F. A. J. ARMSTRONG. 1974. The chemical analysis of fresh water. Dep. Environ. Fish Mar. Serv. Res. Dev. Dir. Misc. Spec. Publ. No. 25.

STOERMER, E. F., L. SICKO-GOAD, AND D. LAZINSKY. 1981. Synergistic effects of phosphorus and heavy metal loadings on Great Lakes phytoplancton, p. 156–172. Proc. 3rd USA–USSR symposium on theoretical aspects of aquatic toxicology, Leningrad.

SUNDA, W., AND R. L. GUILLARD. 1976. The relationships between cupric ion activity and the toxicity of copper to phytoplankton. J. Mar. Res. 34: 511–529.

# Predicting the Effect of Macrobenthos on the Sediment/Water Flux of Metals and Phosphorus

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Starkel, W. M. 1985. Predicting the effect of macrobenthos on the sediment/water flux of metals and phosphorus. Can. J. Fish. Aquat. Sci. 42: 95–100.

The log-transformed flux rates of iron, manganese, and phosphorus in a small, softwater lake were linearly related to the biomass of *Chaoborus* and chironomid larvae. Flux rates were measured by measuring the change in chemical concentrations in the water overlying the sediment of undisturbed cores incubated in situ for 1–2 d. Predicted flux rates of iron and phosphorus at average pelagic densities of animals were enhanced at least twofold over predicted fluxes for diffusion alone. Macroinvertebrates had no apparent effect on flux rates of dissolved oxygen, dissolved inorganic carbon, potassium, or sodium.

Nous avons observé une relation linéaire entre le logarithme du flux de molécules de fer, de manganèse et de phosphore et la biomasse des *Chaoborus* et des larves de chironomidés dans un petit lac. Nous avons déterminé le flux en mesurant les variations de la concentration des composantes chimiques de l'eau environnant des carottes de sédiments laissées in situ 1 ou 2 jours. La valeur du flux de molécules de fer et de phosphore que nous avons prévue pour des populations d'animaux pélagiques de densité moyenne représentait au moins le double de la valeur escomptée du flux de diffusion seul. Les macroinvertébrés n'avaient pas d'effet apparent sur le flux d'oxygène dissous, de carbone, de potassium ou de sodium inorganique dissous.

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Exchange between sediments and water is an important aspect of the movement of materials and energy in lakes. Exchanges may be estimated by input–output models for a whole lake, or determined by investigation of the conditions and processes at the sediment/water interface. Kortmann (1980) used both of these approaches in Dunham Pond, CT for estimating flux rates for silica, nitrogen, phosphorus, and iron. The current study adds detail to these estimates in terms of the effect of macrobenthos on exchange processes. Regression techniques are used to quantify the relationship between experimentally determined flux rates and animal density. Regressions have the potential advantage of partitioning variance among the physical, chemical, and biological predictors of flux rate.

This study was designed to determine the effect of zoobenthic activity on the flux rates of a variety of chemical species. These were chosen to represent (1) conservative chemical species (K, Na), (2) redox-active metals (Fe, Mn), (3) metabolic gases ($O_2$, $CO_2$), and (4) nutrients (P). Many benthic invertebrates affect fluxes of oxygen, phosphorus, and some toxic metals (Graneli 1979a; Gallepp 1979; review by Petr 1977), and chironomid larvae affect benthic fluxes of iron and manganese (Graneli 1979b). Jacobsen (1977, cited in Kamp-Nielsen et al. 1982) investigated the effect of *Chaoborus* on sediment/water exchange and found no effect on phosphorus flux in Lake Esrom sediments. However, the density of *Chaoborus* in Lake Esrom is much lower than in Dunham Pond.

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## Materials and Methods

Dunham Pond is a small (4.7 ha) lake located in the eastern crystalline highlands of Connecticut (see descriptions in Rich 1979; Kortmann 1980). Dunham has a maximum depth of 4.5 m and a littoral zone that extends to 1.5 m depth. The profundal area represents 63% of the total surface area. The surficial profundal sediment has a high organic content (60% of dry mass) and is over 50% water. The sediment surface between the 1.5- and 3.5-m contours is frequently covered with an algal mat. Light is strongly attenuated by dissolved humic material, and 1% light seldom reaches 2.5 m. This results in stable summer stratification of the water column. A small wind fetch and protection by surrounding hills produces a small coefficient of eddy diffusion (Rich 1979). Anoxia occurs below 2.5 m from mid-July through mid-September. The profundal macrobenthos is composed mainly of *Chaoborus punctipennis* larvae at densities often exceeding 20 000/$m^2$. Chironomid larvae are much less abundant but account for 5% of the total mass of macroinvertebrates. *Chironomus tentans* and *C. plumosus* are the most abundant chironomids (Pallotti 1976). Other groups are poorly represented.

I initially attempted to determine the effect of *Chaoborus* burrowing and migration activity on sediment/water exchange of total iron, ferrous iron, dissolved inorganic carbon (DIC), oxygen, sodium, and potassium. Total phosphorus and total manganese were analyzed in later experiments. Flux rates were determined by measuring changes in chemical concentrations in the overlying water of undisturbed cores. Cores were taken with 17.3-$cm^2$ Plexiglas liners attached to a weighted Kajak-type

corer. For each experiment I took four control cores at 3.5 m at night while most of the animals were feeding in the water column. Four experimental cores were taken the following morning. At this time I took initial water samples from all cores. The overlying water was stirred gently enough to prevent sediment from being resuspended, and samples were withdrawn from a point 5 cm above the sediment surface. I then slid the core liners down over their supports so that air bubbles could be excluded when the cores were sealed with Saran wrap. All cores were suspended in the lake at 3.5 m and incubated for 24 or 48 h. After incubation I carefully pulled the cores into a boat, broke the seals, and sampled the overlying water in the same manner as for the initial samples. All cores that had resuspended sediment or broken seals were excluded from the study. Immediately after sampling the cores were sieved (0.5 mm), and the retained animals were counted and classed by size.

*Charoborus* larvae migrate on an internal, diurnal rhythm adjusted by photoperiod (LaRow 1968), and migration was expected to proceed normally within the sealed cores. I confirmed this by laboratory observations of fresh cores not used in the experimental procedure.

Animal densities in the lake were estimated by sampling semimonthly from June to December and bimonthly at other times of the year. I divided the profundal area into three contour intervals (1.5–3.0, 3.0–4.0, and 4.0–4.5 m) and took three or four random core samples within each interval. A 17.3-$cm^2$ core was used to sample the dense *Chaoborus* population. Cores were sieved (0.5 mm), and animals picked by hand. *Chaoborus* larvae were counted by instar, and since instar determination was not practicable for chironomids, each chironomid larva was measured. Chironomid body lengths (BL) were converted to fresh masses (FM) using the following equation:

$$\ln (FM) = 2.38 \ln (BL) - 4.12$$

where FM is in milligrams and BL is millimetres. For this equation, $r^2 = 0.98$, $p \ll 0.001$, slope SE = 0.08, and intercept SE = 0.21. Fresh masses were measured on live animals blotted with Kimwipes, and dry masses were determined following drying at 60°C for 24 h. All masses were determined with an analytical balance (to within 0.1 mg).

Total iron and total manganese were measured by atomic absorption spectrophotometry, and sodium and potassium by emission spectrophotometry. Ferrous iron was determined colorimetrically by the addition of 1,10-phenanthroline (American Public Health Association 1981). Samples for total phosphorus (water and whole animals) were digested in sulfuric acid and the concentration determined colorimetrically by the antimony–molybdate method with ascorbic acid reduction (Golterman et al. 1978). Oxygen content was measured by the azide modification of the Winkler method, and DIC by infrared spectrophotometry. I calculated flux rates using the following formula:

$$F = \frac{(C_f - C_i)V}{\Delta t \cdot A}$$

where $F$ = flux rate (millimoles per square metre per day) out of sediment into overlying water, $C_f$ = final molar concentration (millimoles per cubic metre) in overlying water, $C_i$ = initial concentration, $V$ = volume (cubic metres) of overlying water, $\Delta t$ = incubation time (days), and $A$ = cross-sectional area (square metres) of core.

### Statistical Procedures

I split the data a priori by material (i.e. total iron, phosphorus, etc.) and by the oxygen condition of the water overlying the sediments. I used $O_2$ condition because chemical conditions differ markedly near the sediment boundary depending on the redox conditions of the overlying water. The criterion for anoxia was no detectable dissolved $O_2$ in the hypolimnion. (Often, a trace of $O_2$ was found in the overlying water of sediment cores due to the activity of benthic algae.) These splits resulted in both oxic and anoxic models for each chemical species measured.

Since some flux variables were not normally distributed, I used transformed flux data for fitting the models. Flux data were transformed so that residuals from the fitted models came from a distribution that adequately approximated the normal. The criterion for an adequate approximation of normality was that the cumulative distribution of the residuals should form a straight line when plotted on graph paper having a normal probability scale. If $n$ was small, these plots of residuals were compared with several plots of the same number of points drawn randomly from a normal distribution.

The model selection procedure began with the variables for animal density. Chaoborid number, chaoborid fresh mass, chironomid number, chironomid fresh mass, total numbers, and total fresh mass were included for selection. The selection criterion for one variable models was maximum $r^2$. A two-variable model was selected if the $r^2$ was increased significantly ($p = 0.05$) over the "best" one-variable model. Only models with one chaoborid variable and one chironomid variable were considered for two-variable models.

After selecting the variable for animal density, other predictor variables were considered. Since I combined data from more than one experiment for some of the models, environmental factors become potential variables. These environmental factors may include redox conditions, temperature, light, and other factors influencing sediment conditions. Because such variables may affect flux and may be correlated with animal density, some relationships between animal density and flux may be spurious. Redox conditions and associated changes in concentration gradients are partially accounted for by splitting the data between oxic and anoxic conditions, as previously mentioned. Temperature is probably the most important of the remaining variables, and should be correlated with other seasonal changes. Therefore, I used temperature, together with animal density, as a predictor variable in multiple regression models for all measured fluxes. Partial plots and tests of significance for parameters were used to evaluate the importance of temperature and animal densities.

The criterion for selection of a final model was a significant contribution (test of parameter = 0, $p = 0.05$) of an animal density variable to the model. Oxygen and DIC flux rates, although initially related to animal density, failed to meet this criterion. Final model residuals were plotted against predicted values and inspected for indications of nonhomogeneity of variance and nonlinearity.

## Results

### Model Selection

Five experiments were conducted in oxic conditions during the spring and fall, and three during summer anoxia. Sodium and potassium fluxes were measured in all experiments. These

TABLE 1. Sediment/water exchange rates as functions of animal density in Dunham Pond cores. Flux rates have units of mmol·m$^{-2}$·d$^{-1}$; independent variables have units of g fresh mass/m$^2$. A flux of 0.693 corresponds to a zero flux in untransformed data. Positive flux indicates movement out of the sediments into the water. TMASS = mass of macrobenthos; CHIRMASS = mass of chironomids; CHAOMASS = mass of *Chaoborus*; SE = one standard error.

| Flux rate | = | Slope (SE) | × | Indep. variable | + | Slope (SE) | × | Indep. variable | + | Intercept (SE) | $n$ | (No. of exps) | $r^2$ | $p$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Oxic models | | | | | | | | | | | | | | |
| ln (total Fe flux + 2) | | 0.0053 (0.0019) | | TMASS | | | | | | 0.876 (0.054) | 33 | (5) | 0.198 | 0.009 |
| ln ($Fe^{2+}$ flux + 2) | | 0.0411 (0.0024) | | CHIRMASS | | 0.0035 (0.0014) | | CHAOMASS | | 0.715 (0.038) | 18 | (3) | 0.963 | <0.001 |
| ln (total Mn flux + 2) | | 0.00030 (0.00003) | | TMASS | | | | | | 0.690 (0.001) | 6 | (1) | 0.968 | <0.001 |
| ln (total P flux + 2) | | 0.00152 (0.00061) | | TMASS | | | | | | 0.693 (0.021) | 13 | (2) | 0.364 | 0.029 |
| Anoxic models | | | | | | | | | | | | | | |
| ln (total Mn flux + 2) | | −0.0061 (0.0024) | | TMASS | | | | | | 0.778 (0.019) | 6 | (1) | 0.868 | 0.007 |
| ln (total P flux + 2) | | 0.00081 (0.00032) | | TMASS | | | | | | 0.704 (0.005) | 6 | (1) | 0.613 | 0.066 |

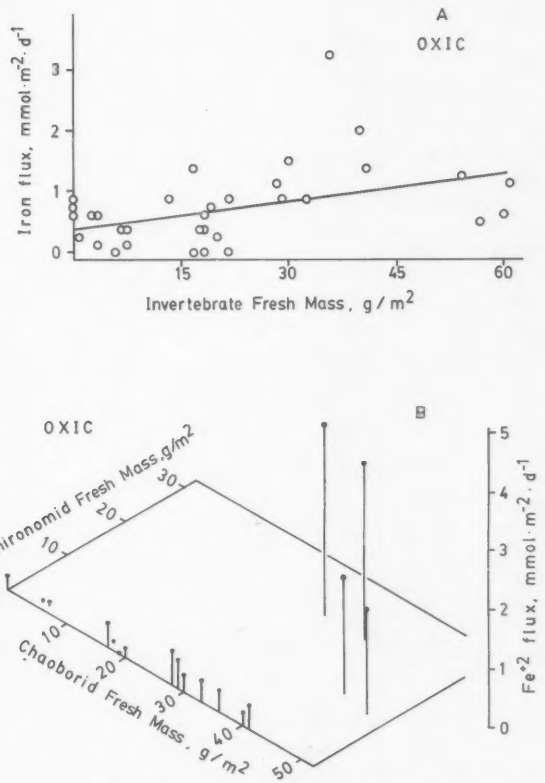


FIG. 1. (A) Scatter plot of total iron flux on invertebrate mass for Dunham Pond cores. The line is based on the relationship ln (flux + 2) = 0.0053 TMASS + 0.876 (Table 1). (B) Three-dimensional plot of ferrous iron flux on chironomid mass and chaoborid mass. Points on the plane are determined by the masses of the two animal groups. Height above the plane represents the flux rate. A positive flux indicates movement out of the sediment into the water.

fluxes were predominantly positive (out of the sediment) but showed no relationship to animal density. DIC and oxygen fluxes were measured in seven experiments. In initial simple regressions, oxygen flux was directly related to animal density and DIC flux was indirectly related to animal density. These relationships were counterintuitive and apparently spurious because temperature was the only significant predictor in a multiple regression model.

I determined total iron fluxes in all experiments, and ferrous iron in the last six experiments. These fluxes were directly related to animal mass variables in oxic conditions (Fig. 1; Table 1). In anoxic conditions, iron flux rates were high, but unrelated to animal mass. Total phosphorus fluxes were determined in the last three experiments. Direct relationships between phosphorus flux and animal mass occurred in both oxic and anoxic conditions (Fig. 2; Table 1). Total manganese fluxes were measured in the last two experiments. These fluxes were directly related to animal mass in oxic conditions and indirectly related to animal mass in anoxic conditions (Fig. 3; Table 1).

Models relating the total fresh mass of macrobenthos to total iron, phosphorus, and manganese fluxes had the highest $r^2$ values in most cases (Table 1). The ferrous iron model had a significantly higher $r^2$ when two predictors were used (chironomid fresh mass and chaoborid fresh mass). Note that all flux variables in Table 1 are similarly transformed, allowing direct comparison of slopes and intercepts.

Residuals from the models have no discernable patterns when plotted on predicted values. This indicates that (1) the simple linear regressions adequately fit the data and (2) the homogeneity of variance assumption of least squares regression was not violated. Normal plots and frequency histograms of the residuals indicated that the residuals came from underlying distributions that, as transformed, adequately approximated the normal.

## Animal Data

Average profundal fresh masses (±1 SE, and with the number of samples in parentheses), of macrobenthos were 40.0 ± 5.3 g/m$^2$ (100) in oxic conditions and 18.1 ± 3.2 g/m$^2$ (54)

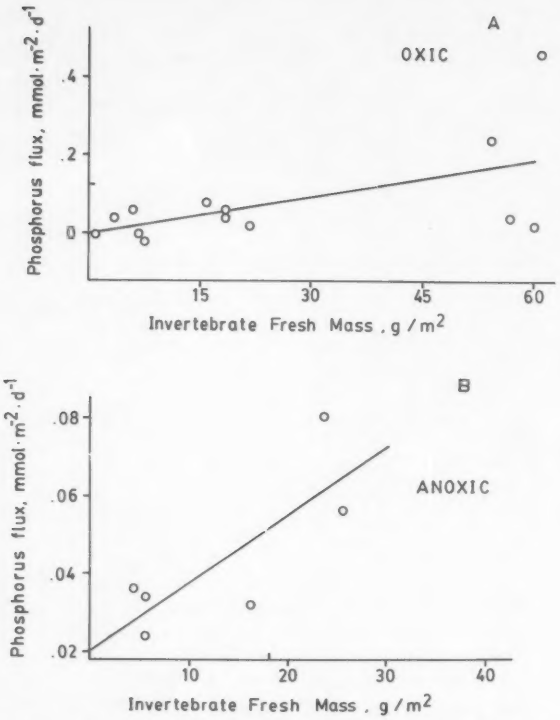


FIG. 2. Scatter plots of total phosphorus flux on invertebrate mass for contrasting hypolimnetic oxygen conditions. (A) The line is based on the relationship ln (flux + 2) = 0.00152 TMASS + 0.693 (Table 1); (B) the line is based on the relationship ln (flux + 2) = 0.00081 TMASS + 0.704 (Table 1).

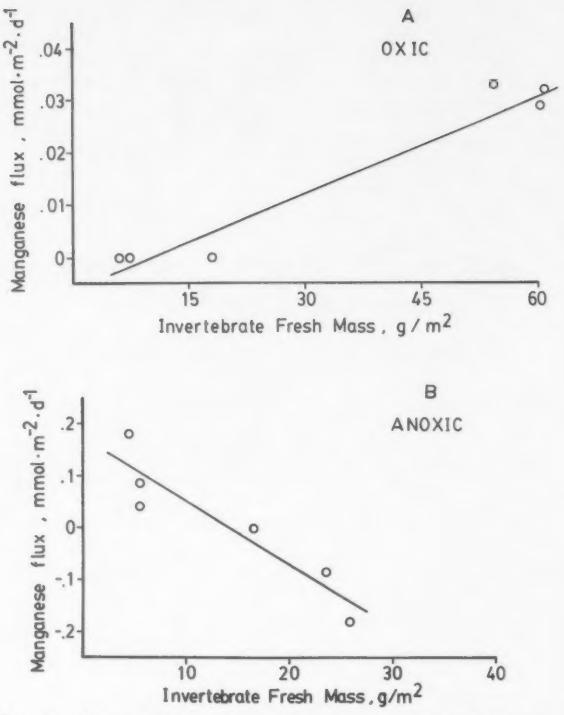


FIG. 3. Scatter plots for total manganese flux on invertebrate mass for contrasting hypolimnetic oxygen conditions. (A) The line is based on the relationship ln (flux + 2) = 0.00030 TMASS + 0.690 (Table 1); (B) the line is based on the relationship ln (flux + 2) = −0.0061 TMASS + 0.778 (Table 1).

when the water overlying the sediment was anoxic. Chironomids represented 5% of the mass in both conditions. Average fresh masses at 3.5 m depth, where experimental cores were taken, were 25.0 ± 3.8 g/m² (33) (1% chironomids) under oxic conditions and 29.0 ± 3.9 g/m² (11) (0% chironomids) under anoxic conditions.

Most (85%) of the *Chaoborus* individuals counted were 4th instar larvae having a fresh mass of 1.91 ± 0.04 mg/individual. Phosphorus contents of chaoborids and chironomids were 1.12 and 1.24 μg P/mg fresh mass, respectively. Dry mass was 9.53% of fresh mass for 4th instar *Chaoborus* and 13.5% of fresh mass for chironomids.

## Discussion

Published data involving several lakes corroborate predictions of the Dunham Pond models for phosphorus and iron. Gallepp's (1979) data indicate a linear relationship between chironomid density and the flux rate of phosphorus from Lake Mendota sediment into oxic water. An estimated regression through these data has a slope of about 0.00075, if the units are transformed to those used in my models. This value is within 1.3 SE of the slope for the oxic phosphorus model for Dunham Pond. Graneli's (1979b) data indicate iron flux rates of 1.03 and 1.92 mmol·m$^{-2}$·d$^{-1}$ for cores from Lakes Trummen and Arungen, respectively. These rates pertain to the period immediately after the introduction of chironomid larvae to the cores. They compare favorably with the flux rate predicted by the total iron model from Table 1, which is 0.89 mmol·m$^{-2}$·d$^{-1}$.

The Dunham Pond models may be interpreted in terms of diffusion theory. Fick's first law of diffusive transport may be expressed as follows (Berner 1976):

$$J_i = \phi_0 D_0 \left.\frac{\partial C}{\partial x}\right|_x = 0$$

where $J_i$ = flux rate of substance $i$ (positive out of the sediment), $D_0$ = diffusion coefficient for $i$ at the interface, $\phi_0$ = sediment porosity at the interface, $C$ = concentration of $i$, and $x$ = sediment depth. The models in Table 1 may be seen as expressions of $D_0$. As such, the slopes of the models represent the magnitude of the enhancement of diffusion by animal activity. The intercepts of the models estimate the flux rates from simple diffusion alone. Also, the effects of animals on flux rate should be more apparent as the concentration gradient across the sediment/water interface increases.

The slopes of the models in Table 1 represent the magnitude of the effect of animal mass on the exchange rate across the sediment/water interface. The oxic iron and phosphorus models appear to differentiate the effects of the animal groups. The model for ferrous iron includes terms for both chaoborid fresh mass and chironomid fresh mass, with the chironomid term having a slope an order of magnitude higher. Since chironomids are filter-feeders and full-time inhabitants of the sediment, it is possible that their rate of activity is higher than that of the chaoborids, which do not feed in the sediments.

TABLE 2. Uncoded intercepts and predicted flux rates for Fe and P models from Table 1. Predicted flux rates are based on the following average masses of profundal macrobenthos: oxic conditions, 40.0 g fresh mass/$m^2$ (5.2% chironomids); anoxic conditions, 18.1 g fresh mass/$m^2$. Positive fluxes indicate movement out of the sediment into overlying water.

| Material | Intercept ($mmol \cdot m^{-2} \cdot d^{-1}$) | Predicted flux ($mmol \cdot m^{-2} \cdot d^{-1}$) |
|---|---|---|
| Oxic conditions | | |
| Total Fe | 0.40 | 0.97 |
| Ferrous Fe | 0.04[a] | 0.54 |
| Total P | 0 | 0.125 |
| Anoxic conditions | | |
| Total P | 0.021 | 0.051 |

[a]Intercept not significantly different from zero.

The intercepts of the models represent the fluxes due to simple diffusion alone. They can be compared with independent estimates of flux from diffusion alone obtained by substituting known values into the equation for Fick's law. This is possible for ferrous iron and dissolved phosphorus, because sediment and overlying water concentrations are available for these materials in Dunham Pond (Kortmann 1980). Analysis of Kortmann's data yields the following average gradients (±1 SE, $n$ in parentheses) across the sediment/water interface:

| | |
|---|---|
| Ferrous Fe | |
| Oxic | $5.0 \pm 1.5 \times 10^2$ mmol·m$^{-4}$ (8) |
| Anoxic | $-7.0 \pm 2.7 \times 10^2$ mmol·m$^{-4}$ (2) |
| Dissolved P | |
| Oxic | $5.7 \pm 3.7 \times 10^2$ mmol·m$^{-4}$ (8) |
| Anoxic | $0.7 \pm 0.6 \times 10^2$ mmol·m$^{-4}$ (2) |

Porosity was assumed to be 0.75, and values for $D_0$ were taken from Li and Gregory (1974). The following fluxes for simple diffusion were calculated: oxic $Fe^{2+} = 0.015$ mmol·$m^{-2}$·$d^{-1}$, oxic P = 0.022 mmol·$m^{-2}$·$d^{-1}$, and anoxic P = 0.0027 mmol·$m^{-2}$·$d^{-1}$. All of these values are within 2 SE of the intercepts (when uncoded) for the appropriate models in Table 1.

The effects of animals on flux rates appear to relate directly to the concentration gradients listed in the preceding paragraph. Gradients are low (for flux out of the sediments) during periods of anoxia and high during oxic periods for both ferrous iron and phosphorus. Correspondingly, there is no relationship between iron flux and animal density during anoxia, and the slope of the phosphorus model is lower during anoxia (Table 1). A direct relationship between animal effects and concentration gradients may be explained as follows. Redox-active substances such as iron, manganese, and phosphorus will generally have high concentration gradients at or near the sediment/water interface. This condition is due to the accumulation of these substances in sediment pore water and is enhanced when the overlying water is oxic (Wetzel 1983). Animal activity at the interface may be expected to act upon these gradients, increasing the flux rate. In Dunham Pond, animal activity increases iron and phosphorus flux at least twofold, as shown in Table 2.

The manganese models may also be interpreted by seasonal changes in concentration gradients. The anoxic manganese model has a negative slope, unlike all the others in Table 1, including the oxic manganese model. This suggests a negative concentration gradient across the sediment/water interface during anoxia, and a positive gradient in oxic conditions. Loss of manganese from the sediments during oxic conditions was also found by Davidson et al. (1982) for Esthwaite Water, and their findings indicate that a negative gradient may occur during summer anoxia.

An alternative explanation for the effect of zoobenthos on phosphorus flux is that it is caused by the animals' excretion (see Gardner et al. 1981; Gallepp 1979). If Johannes' (1964) regression is used to estimate the phosphorus excretion rates of Dunham Pond animals, they are an order of magnitude higher than the phosphorus fluxes predicted by my models. However, the excretion rate of iron would be very low relative to phosphorus, because the molar Fe:P ratio of plankton is about 0.05 (Wetzel 1983). Also, the flux rates of iron in Dunham Pond are at least five times higher than the flux rates of phosphorus (see Table 2). Therefore, the mixing caused by burrowing or filter-feeding appears to account for the enhanced flux of iron. Because both iron and phosphorus have concentration gradients across the sediment/water interface, a mixing effect, rather than excretion alone, is implicated for the effect of animals on phosphorus flux. This mechanism of mixing across a gradient is supported by data in Holdren and Armstrong (1980). They found that chironomid activity resulted in high rates of phosphorus release from Lake Mendota sediments only when the phosphorus concentration of the overlying water was kept low.

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## References

AMERICAN PUBLIC HEALTH ASSOCIATION. 1981. Standard methods for the examination of water and wastewater, 15th ed. American Public Health Association, Washington, DC.

BERNER, R. A. 1976. The benthic boundary from the viewpoint of a geochemist, p. 33–55. *In* I. N. McCave [ed.] The benthic boundary layer. Plenum Press, New York, NY.

DAVISON, W., C. WOOLF, AND E. RIGG. 1982. The dynamics of iron and manganese in a seasonally anoxic lake; direct measurement of fluxes using sediment traps. Limnol. Oceanogr. 27: 987–1003.

GALLEPP, G. W. 1979. Chironomid influence on phosphorus release in sediment–water microcosms. Ecology 60: 547–556.

GARDNER, W. S., T. F. NALEPA, M. A. QUIGLEY, AND J. M. MALCZYK. 1981. Release of phosphorus by certain benthic invertebrates. Can. J. Fish. Aquat. Sci. 38: 978–981.

GOLTERMAN, H. L., R. S. CLYMO, AND M. A. M. OHNSTAD. 1978. Methods for physical and chemical analysis of fresh waters. Blackwell Scientific Publications, Oxford. 213 p.

GRANELI, W. 1979a. The influence of *Chironomus plumosus* larvae on the oxygen uptake of sediment. Arch. Hydrobiol. 87: 385–403.

1979b. The influence of *Chironomus plumosus* larvae on the exchange of dissolved substances between sediment and water. Hydrobiologia 66: 149–159.

HOLDREN, G. C. JR., AND D. E. ARMSTRONG. 1980. Factors affecting phosphorus release from intact lake sediment cores. Environ. Sci. Technol. 14: 79–87.

JOHANNES, R. E. 1964. Phosphorus excretion and body size in marine animals: microzooplankton and nutrient regeneration. Science (Wash., DC) 146: 923–924.

KAMP-NIELSEN, L., H. MEJER, AND S. E. JORGENSEN. 1982. Modelling the influence of bioturbation on the vertical distribution of sedimentary phosphorus in L. Esrom. Hydrobiologia 91: 197–206.

KORTMANN, R. W. 1980. Benthic and atmospheric contributions to the nutrient budgets of a soft-water lake. Limnol. Oceanogr. 25: 229–239.

LAROW, E. J. 1968. A persistent diurnal rhythm in *Chaoborus* larvae. I. The nature of the rhythmicity. Limnol. Oceanogr. 13: 250–256.

LI, Y.-H., AND S. GREGORY. 1974. Diffusion of ions in sea water and in deep-sea sediments. Geochim. Cosmochim. Acta 38: 703–714.

PALLOTTI, B. L. 1976. The effect of the several physical and chemical factors upon the distribution of benthic macroinvertebrates in Dunham Pond, Connecticut. M.S. thesis, University of Connecticut, Storrs, CT. vii + 78 p.

PETR, T. 1977. Bioturbation and exchange of chemicals in the mud–water interface, p. 216–226. *In* H. L. Golterman [ed.] Interactions between sediments and fresh water. Dr. W. Junk bv Publishers, The Hague.

RICH, P. H. 1979. Differential $CO_2$ and $O_2$ benthic community metabolism in a soft-water lake. J. Fish. Res. Board Can. 36: 1377–1389.

WETZEL, R. G. 1983. Limnology. CBS College Publishing, Philadelphia, PA. xii + 767 p.

# Initial Changes in Use of Space and Food by Experimentally Segregated Populations of Dolly Varden (*Salvelinus malma*) and Cutthroat Trout (*Salmo clarki*)

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Dolly Varden (*Salvelinus malma*) ($N$ = 881) and cutthroat trout (*Salmo clarki*) ($N$ = 1571) were captured from a native lacustrine sympatric stock and transferred to two nearby lakes, formerly fishless, to establish allopatric populations with genetic backgrounds similar to the donor stock. Nearshore (5- and 10-m depth contours) vertical distributions of segregated Dolly Varden and cutthroat trout, between spring and autumn of the first 18 mo after transfer, did not differ significantly from those in their sympatric lake. Dolly Varden were captured mainly near the bottom while cutthroat trout were more evenly distributed throughout the water column. Nevertheless, initially the allopatric Dolly Varden rapidly became highly planktivorous, virtually eliminating midwater populations of *Chaoborus trivittatus* and *C. americanus* (third and fourth instar larvae) within a year. They later ate mainly benthic organisms as in the sympatric lake. Although allopatric cutthroat trout had a similar effect on *Chaoborus* larvae in their lake, they also ate more large benthic prey than did those in sympatry with Dolly Varden in the donor lake. These results suggest that while there may be genetic control restricting broad vertical use of space by formerly sympatric Dolly Varden shortly after being placed in allopatry, such control is flexible enough that a highly benthofagous stock in sympatry quickly becomes planktivorous in the absence of cutthroat trout.

Nous avons prélevé des dolly varden (*Salvelinus malma*) ($N$ = 881) et des truites fardées (*Salmo clarki*) ($N$ = 1517) d'un stock sympatrique indigène que nous les avons relâchés dans deux lacs voisins où il n'y avait auparavant pas de poissons afin d'y établir des populations allopatriques possédant les mêmes antécédents génétiques que les stocks donneurs. Au cours des 18 mo suivants, la distribution verticale des populations séparées de dolly varden et de truites fardées dans les eaux de rivage (lignes de profondeur de 5 et 10 m) n'a pas différé de façon significative de celle des populations sympatriques du printemps à l'automne. La plupart des dolly varden ont été capturés près du fond de l'eau, tandis que les truites fardées étaient plus uniformément dispersées dans la colonne d'eau. Néanmoins, les dolly varden allopatriques à l'origine ont rapidement adopté un régime fortement planctivore, éliminant en un au pratiquement toutes les populations de *Chaoborus trivittatus* et de *C. americanus* (troisième et quatrième stades larvaires) des eaux intermédiaires. Par la suite, ils se sont surtout nourris d'organismes benthiques comme leurs congénères des populations sympatriques. Les truites fardées allopatriques ont eu le même effet sur les larves de *Chaoborus* du lac où elles ont été relâchées, mais elles ont mangé de plus gros organismes benthiques que leurs congénères en sympatrie avec les dolly varden dans le lac donneur. Ces résultats indiquent qu'il se peut qu'un mécanisme génétique limite la dispersion verticale des dolly varden anciennement sympatriques quelque temps après qu'ils aient été placés en allopatrie, mais que ce mécanisme est suffisamment adaptable pour que les poissons de populations sympatriques à régime fortement benthofage deviennent rapidement planctivores en l'absence de truites fardées.

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Study of competitive relationships between closely related species pairs has commanded the attention of fish ecologists, particularly in North America and Scandinavia, for several decades. One way to study these relationships is to compare species pairs coexisting sympatrically in a single lake and separately (allopatrically) in different lakes (Nilsson 1963; Andrusak and Northcote 1971; Nilsson and Northcote 1981). A common observation, especially in salmonids with a high degree of ecological and behavioral "plasticity," is that niche preferences for space and food change in the presence or absence of interacting species — broadening in allopatry and narrowing in sympatry. Whether these changes result from learned (interactive) processes or from genetic processes (Brian 1956; Nilsson 1967) usually cannot be determined in such comparative studies.

Some of the difficulty involved in making inferences about interactive or selective segregation by means of whole lake comparisons may be overcome by experimentally forming two allopatric populations of similar genetic background as the donor sympatric population. If possible, the lakes involved in

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such a transfer should be similar limnologically and should not contain other species of fish to complicate interactions. Three lakes in the University of British Columbia Research Forest were suited for such an experiment (Northcote and Clarotto 1975), and appropriate species transfers were accomplished between autumn 1974 and spring 1976 to establish reproducing, allopatric populations from a known nearby sympatric stock. We compared initial patterns of space and food use by the two allopatric populations of Dolly Varden (*Salvelinus malma*) and cutthroat trout (*Salmo clarki*) with those occurring at the same time (1975 and 1976) in the sympatric population.

## Materials and Methods

After an unsuccessful attempt to collect Loon Lake spawners to propagate fry for transfer to the recipient fishless lakes, we captured and transferred 1571 subadult to adult cutthroat trout to Eunice Lake and 881 Dolly Varden to Katherine Lake over an 18-mo period starting in October 1974.

Fish were caught in Loon Lake in two modified Beamish trap nets (Beamish1973) and in a small purse seine. The fish were kept in a holding pen in Loon Lake and transferred, as numbers warranted, in aerated 40-L containers to the appropriate lake.

The vertical distribution of fish in all lakes was recorded by their capture position in 5- and 10-m-deep monofilament nylon gill nets marked at 1-m depth intervals. Each net consisted of three 5-m-long sections of 25-, 38-, and 51-mm stretched mesh. The nets were fished parallel to shore from surface to bottom at 5- and 10-m stations and set approximately once a month from July to October 1975 and from May to August 1976. Dolly Varden data collected in 1972 from Loon Lake were also used because of small sample sizes in the later years.

We did not wish to initially remove large numbers to determine spatial distribution patterns because only a few hundred fish were introduced to establish reproducing populations in each allopatric lake. Consequently, fish catches were combined over all seasons or into spring (May and June), summer (July and August), and autumn (September and October) netting periods, where numbers permitted, to compare vertical distribution in sympatry and allopatry. Furthermore, because previous studies had shown that in sympatry Dolly Varden occupied deep waters close to the bottom whereas cutthroat trout used midwater to near-surface regions (Andrusak and Northcote 1970, 1971; Armitage 1973), the vertical depth intervals at 5- and 10-m contours were divided into two zones, one close to the bottom (4–5 m at the 5-m contour, 8–10 m at the 10-m contour) and the other representing midwater to surface regions. This partitioning of depths permitted statistical comparisons to determine whether or not catches were distributed proportionally between the selected depth intervals.

Fish stomachs were preserved in formalin and later transferred to 70% ethanol for examination. Contents of individual stomachs (lower esophagus to pyloric sphincter) were sorted into major prey categories under 25–50× magnification. The volume of each category was measured by volume displacement in a graduated centrifuge tube, or for small amounts in a graduated 1-mL cylinder accurate to 0.05 mL. Volumes less than 0.05 mL were recorded as 0.001 mL. Mean percent compositions by frequency and volume were determined by summing individual percentages for each prey category in the diet of each fish and dividing by the number of fish containing food (Windell 1971).

Prey were grouped into four major categories: benthos, midwater, fish, and surface (mainly terrestrial insects). Large benthic organisms, such as leeches and the pupae and nymphs of Trichoptera, Plecoptera, and Coleoptera, were separated from small benthos, such as *Pisidium*, gastropods (small lymnaeids), amphipods (*Hyalella*), and chironomid larvae. *Chaoborus* larvae were recorded as a separate midwater form, as they were planktonic at all times in Katherine and Eunice lakes and probably at night in Loon Lake. Other midwater forms were crustacean zooplankton (identified to species), dipteran pupae, and other aquatic insects (mainly notonectids and corixids).

TABLE 1. Physical and chemical (limnetic surface water) characteristics of the study lakes (see Northcote and Clarotto 1975 for details).

| Characteristics | Loon | Eunice | Katherine |
|---|---|---|---|
| Elevation (m) | 340 | 480 | 505 |
| Surface area (ha) | 48.6 | 18.2 | 20.7 |
| Maximum depth (m) | 62 | 42 | 29 |
| Mean depth (m) | 27.5 | 15.8 | 7.5 |
| Epilimnion depth (m) | 8 | 6 | 6 |
| Secchi transparency (m) | 9 | 10 | 9 |
| Colour (Pt units) | 5 | 15 | 15 |
| Total dissolved solids ($mg \cdot L^{-1}$) | 32 | 16 | 15 |
| pH | 6.7 | 6.4 | 6.6 |

### Study Lakes

The three lakes are in the U.B.C. Research Forest (49°19′N, 122°34′W) about 50 km east of Vancouver, B.C. General physical–chemical characteristics of the lakes are summarized in Table 1.

The lakes share at least five species of limnetic cladocerans (*Daphnia rosea*, *Holopedium gibberum*, *Diaphanosoma brachyurum*, *Polyphemus pediculus*, and *Bosmina longirostris*) and one species of calanoid copepod (*Diaptomus kenai*). Two additional limnetic cladocerans (*Leptodora kindti* and *Ceriodaphnia pulchella*), as well as three calanoids (*D. leptopus*, *D. oregonensis*, and *D. tyrrelli*), occur in some but not all of the study lakes. One or two cyclopoid species (*Diacyclops thomasi* and *Tropocyclops prasinus*) also are found in the lakes. The large third and fourth larval instars of *Chaoborus trivittatus* and *C. americanus* form midwater concentration zones at 7–10 m during the day (spring to autumn) in Eunice and Katherine lakes (before fish introduction) and migrate into surface waters at night (Fedorenko and Swift 1972). In Loon Lake, *C. flavicans* larvae are benthic during the day.

Native Dolly Varden and cutthroat trout are present in Loon Lake with adult populations, estimated by Schnabel mark and recapture techniques of about 3100 and 7300 fish, respectively (Hume 1978).

## Results and Discussion

### Use of Space

There are many examples of niche shifts in the presence of cohabiting species (Nilsson 1960, 1963; Andrusak and Northcote 1971; Werner and Hall 1976). In contrast, our experimentally segregated populations did not greatly change the habitats they formerly occupied in sympatry, at least within their first year of allopatry.

In the sympatric lake and after transfer to their allopatric lake, Dolly Varden usually were taken in largest numbers in the

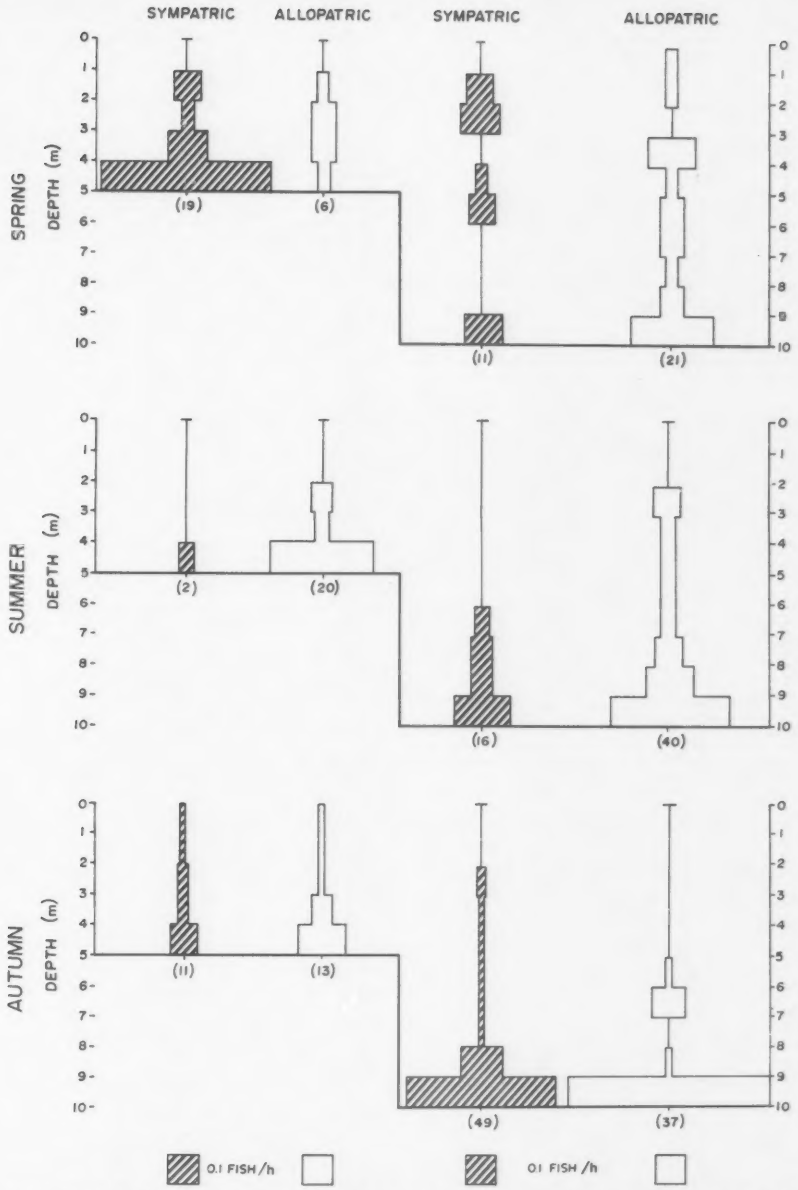


FIG. 1. Vertical distribution of sympatric (Loon Lake) and experimentally allopatric (Katherine Lake) Dolly Varden in surface to bottom gill nets set at 5- and 10-m contour stations. Distributions at each 1-m depth interval expressed as catch per hour (note scales); total catch in parentheses; seasons combined over same years as in Fig. 3.

near-bottom waters whether at the 5- or 10-m depth contour (Fig. 1). This tendency was confirmed statistically by the pooled *G* tests at both 5- and 10-m contours, as well as for two seasonal periods at the 10-m contour (Table 2). In addition, with the data available up to the first year after transfers were completed, no significant differences in Dolly Varden distribution could be demonstrated between the sympatric and allopatric lakes (Table 2).

Catch rates of sympatric cutthroat trout were clearly higher than those of sympatric Dolly Varden in midwater to surface depth intervals, particularly at the 10-m contour (Fig. 1, 2). Close to shore at the 5-m contour, cutthroat trout occupied all depth zones. But during summer, as well as for all seasons pooled, catches in the lowermost metre were significantly higher than would be expected from a proportional distribution to both depth intervals (Table 2). At the 10-m contour, catches for cutthroat trout in the upper 8 m compared with the lower 2 m did not depart significantly from a 4:1 ratio, although for the

TABLE 2. Comparisons ($G$ tests[a]) of vertical distribution between depth intervals[b] and between allopatry and sympatry of fish captured in gill nets set at 5- and 10-m contours in the study lakes (sympatric = Loon Lake; allopatric = Katherine Lake for Dolly Varden, Eunice Lake for cutthroat trout). *Null hypothesis rejected at $P < 0.05$.

| | | Null hypothesis | | | | | |
|---|---|---|---|---|---|---|---|
| | | Catch ratio = 4:1[b] | | | | | |
| | | Sympatric | | Allopatric | | Allopatric = sympatric | |
| Depth contour | Season | $n$ | $G$ | $n$ | $G$ | $n$ | $G$ |
| Dolly Varden | | | | | | | |
| 5 m | Pooled | 32 | 5.10* | 39 | 5.13* | 71 | <0.10 |
| 10 m | Spring and summer | 27 | 3.53 | 61 | 5.61* | 88 | 1.28 |
| | Autumn | 49 | 10.96* | 37 | 9.07* | 86 | 1.29 |
| | Pooled | 76 | 13.82* | 98 | 14.06* | | |
| Cutthroat trout | | | | | | | |
| 5 m | Spring | 73 | 3.41 | 13 | —[c] | | |
| | Summer | 95 | 4.56* | 34 | 1.92 | 129 | <0.10 |
| | Autumn | 100 | 1.63 | 47 | 2.91 | 147 | 0.21 |
| | Pooled | 268 | 9.37* | 94 | 4.50* | | |
| 10 m | Spring | 70 | <0.10 | 12 | —[c] | | |
| | Summer | 107 | 0.63 | 40 | 0.52 | 147 | 1.07 |
| | Autumn | 144 | 1.52 | 46 | <0.10 | 190 | 0.54 |
| | Pooled | 321 | 1.83 | 98 | 0.07 | | |

[a]Transformed data $(\text{catch} + 0.05)^{0.5}$.
[b]4:1 ratio for 5-m depth contour = 0–4 m : 4–5 m; for 10-m depth contour = 0–8 m : 8–10 m.
[c]Sample size was too small for statistical analyses.

spring period there was an obvious concentration in the uppermost 3 m (Fig. 2). Where sample sizes of allopatric cutthroat trout were adequate to permit statistical comparison of the catch, no significant departures from a proportional distribution between the designated upper and lower depth zones were evident at either the 5- or 10-m contour (Table 2). Furthermore, the vertical distribution of cutthroat trout in experimental allopatry did not differ significantly from that in sympatry at either depth.

## Food

No clear or consistent changes in ranking of major prey types were evident in the diet of Dolly Varden during the first 18 mo following their shift from sympatry to allopatry (Fig. 3; Table 3) except for the summer of 1975 when *Chaoborus* were the largest single prey type in the diet of allopatric fish and in 1976 when large benthos dominated their diet.

In sympatry, benthic and midwater prey were nearly equal dietary components of sympatric Dolly Varden during summer (Fig. 3) whereas benthic forms predominated during autumn and midwater forms during spring. Most of the benthic prey of sympatric Dolly Varden in autumn were small (mainly *Hyalella* and chironomid larvae) whereas large forms made greater contributions in summer and spring. Crustacean zooplankters (mainly *Daphnia rosea* and *Diaptomus kenai*) were the most important midwater prey of the sympatric Dolly Varden throughout all seasons examined.

During the first year (1975) after their introduction into Katherine Lake, allopatric Dolly Varden consumed large amounts of midwater *Chaoborus* larvae, an item rarely included in their diet when sympatric. Indeed, the Katherine Lake populations of midwater *C. americanus* and *C. trivittatus* were virtually eliminated within a year after Dolly Varden introduction (Northcote et al. 1978). Following collapse of the chaoborid midwater prey populations, allopatric Dolly Varden in the spring of 1976 shifted to a mainly benthic diet of large prey (leeches and trichopteran larvae) supplemented that summer by midwater zooplankton (almost entirely *Daphnia rosea*) and some chaoborid larvae (Fig. 3). Fish and surface prey were never important items in the diet of either sympatric or allopatric Dolly Varden.

In contrast with that of sympatric Dolly Varden, the major dietary component of sympatric cutthroat trout during all seasons was midwater prey (Fig. 4), for the most part *Daphnia rosea*. Large and small benthic prey rarely contributed more than 10% each, either by volume or by numbers, to the diet of sympatric cutthroat trout. During their first summer (1975) after introduction to Eunice Lake, the allopatric cutthroat trout continued to feed heavily on midwater prey, but this was composed of *Chaoborus* larvae, as well as zooplankton (again mainly *Daphnia rosea*) and dipteran pupae. As in Katherine Lake, the Eunice Lake midwater larval chaoborid populations were virtually eliminated within a year after fish introduction. Although in allopatry the cutthroat trout ate more benthic prey (usually about 20% of their diet by volume) than in sympatry, there was no overall change in the ranking of the prey types in their diet (Table 3). Surface prey formed a larger dietary item for cutthroat trout (allopatric as well as sympatric) in comparison with Dolly Varden (Fig. 3, 4).

The number of Dolly Varden put into Katherine Lake was

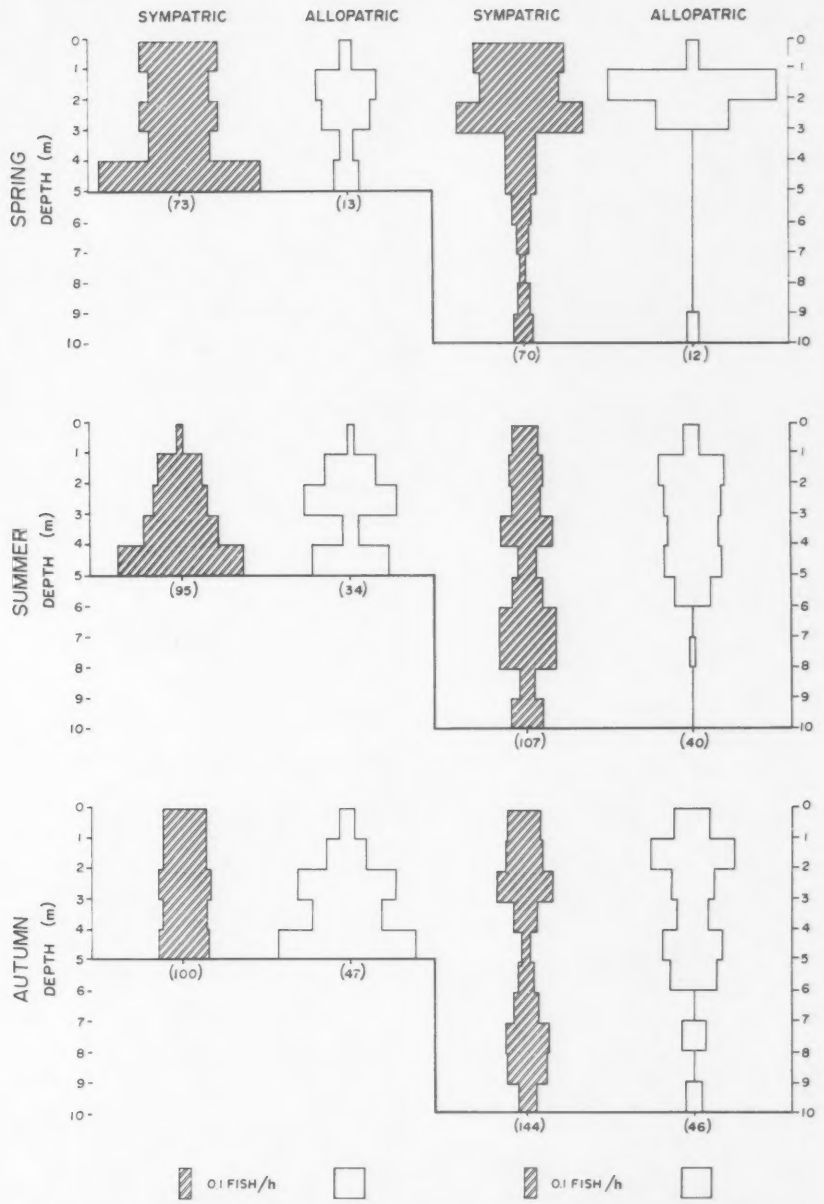


FIG. 2. Vertical distribution of sympatric (Loon Lake) and experimentally allopatric (Eunice Lake) cutthroat trout in surface to bottom gill nets set at 5- and 10-m contour stations. Distributions at each 1-m depth interval expressed as catch per hour (note scale changes); total catch in parentheses; seasons combined over same years as in Fig. 4.

only about half that of cutthroat trout put into Eunice Lake, and yet they were able to effect the decimation of a denser midwater chaoborid population within the same time. This suggests that originally sympatric Dolly Varden, in the absence of cutthroat trout, can quickly become effective planktivores. After the demise of this largest component of the zooplankton community, Dolly Varden then turned to mainly large benthic animals previously unexposed to fish predators. These were taken in even greater volume and frequency than in sympatry.

As for Dolly Varden, the cutthroat trout netting data did not indicate any marked shift in spatial distribution after experimental allopatry. But dietary analysis showed that they must have made frequent temporary excursions to the bottom in order to account for their greater use of large benthic animals compared

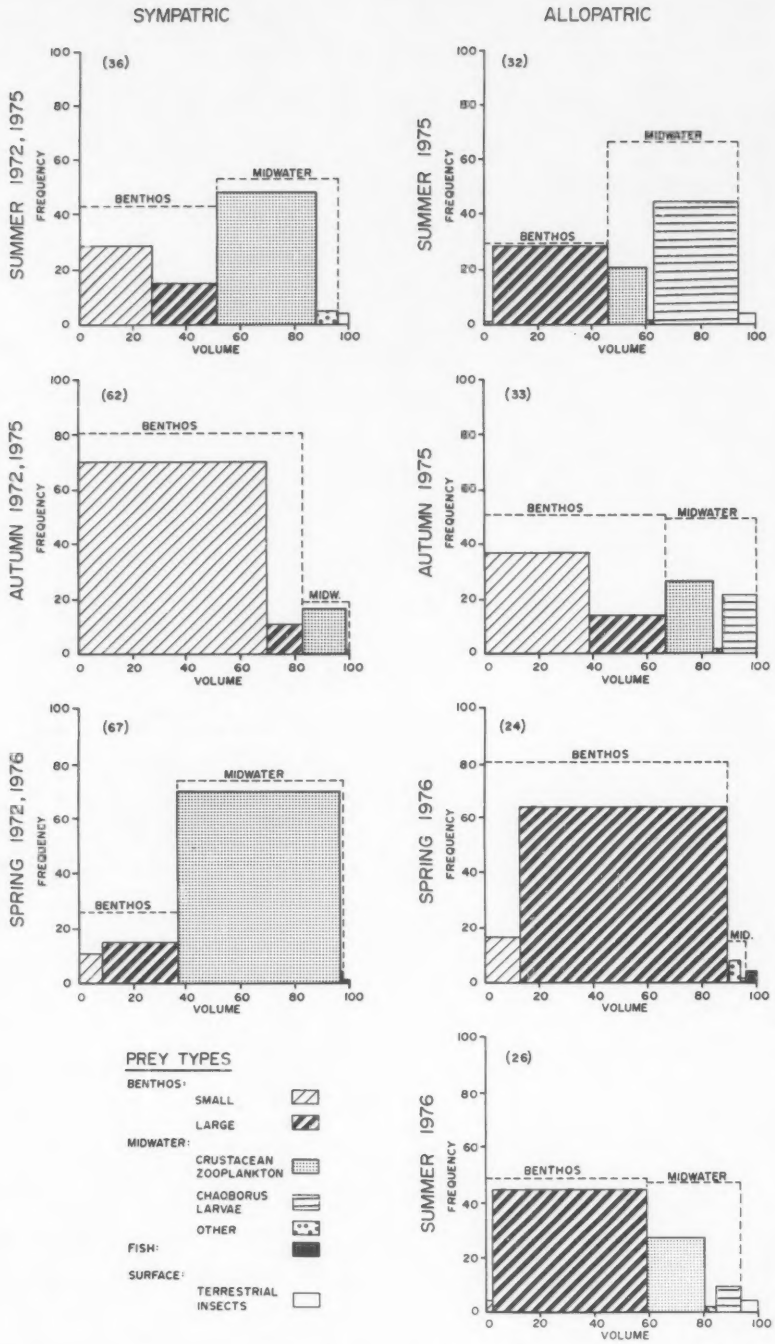


FIG. 3. Percent contribution (volume, frequency) of major prey types to the diet of Dolly Varden when sympatric with cutthroat trout (Loon Lake) and when experimentally allopatric (Katherine Lake). Broken lines indicate total percentages for all benthos and all midwater subgroups. Number of stomachs examined are in parentheses; "other" midwater prey always were >95% dipteran pupae.

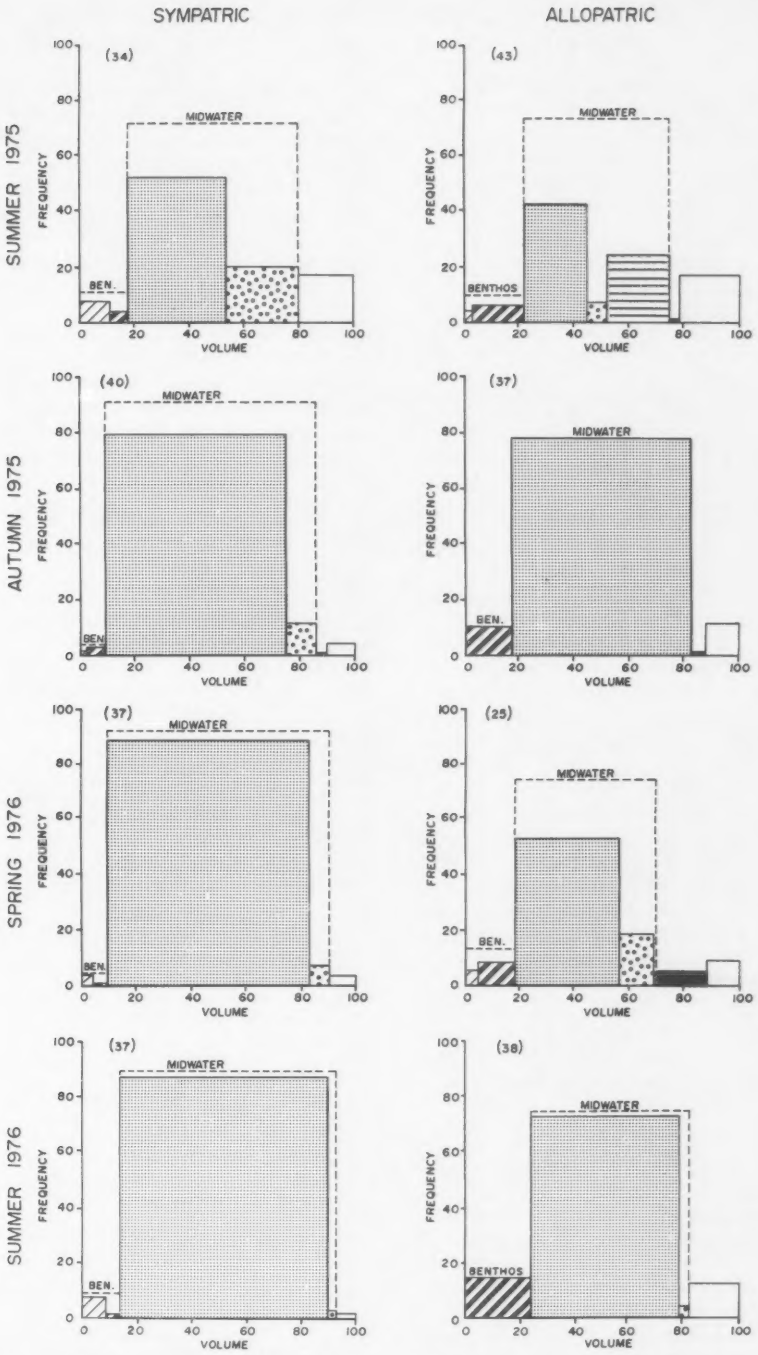


FIG. 4. Percent contribution (volume, frequency) of major prey types to the diet of cuthroat trout when sympatric with Dolly Varden (Loon Lake) and when experimentally allopatric (Eunice Lake). Broken lines indicate total percentages for all benthos and all midwater subgroups. Number of stomachs examined are in parentheses; prey type legend as in Fig. 3.

TABLE 3. Comparison (Spearman's rank correlation test) between allopatry and sympatry of major prey types (as in Fig. 3) for Dolly Varden and cutthroat trout. *Rankings of the prey types in the allopatric and sympatric diets are significantly correlated at $P < 0.05$.

| | Four prey types | | Seven prey types | |
|---|---|---|---|---|
| | Frequency | Volume | Frequency | Volume |
| Dolly Varden | | | | |
| Summer 1975[a] | 1.00* | 0.80 | 0.03 | 0.23 |
| Autumn 1975[a] | 1.00* | 1.00* | 0.78* | 0.86* |
| Spring 1976[a] | 0.60 | 0.60 | 0.66 | 0.21 |
| Summer 1976[a] | 0.80 | 1.00* | 0.54 | 0.36 |
| $-2\Sigma \ln (P)$[b] | 17.03* | 17.03* | 15.52* | 12.02 |
| Cutthroat trout | | | | |
| Summer 1975 | 1.00* | 1.00* | 0.48 | 0.08 |
| Autumn 1975 | 1.00* | 0.80 | 0.71* | 0.86* |
| Spring 1976 | 1.00* | 0.40 | 0.77* | 0.50 |
| Summer 1976 | 1.00* | 1.00* | 0.63 | 0.74* |
| $-2\Sigma \ln (P)$[b] | 23.97* | 16.23* | 19.12* | 18.12* |

[a]Sympatric diet includes data from 1972 and 1975.

[b]If actual probabilities of each test are pooled by this formula, then results can be compared with the chi-square value of 15.51 (df = 8, $P < 0.05$) for an overall test of significance (Sokal and Rohlf 1981).

with that in sympatry. Again, this would suggest that some broadening of the niche of formerly sympatric cutthroat trout did take place when living without Dolly Varden, although not nearly as much as evidenced by long-established allopatric populations.

Limitations in the use of whole lakes to test competitive interactions between these two species may have confounded our results and their interpretation. Although close and similar in many of their limnological characteristics, the two allopatric lakes were different in respect to relative littoral versus limnetic regions. Katherine Lake, as indicated by its lower mean depth, had 47% of its area within the 0–5 m depth zone whereas Eunice Lake had a much greater maximum and mean depth, as well as only 22% of its area less than 5 m deep. These differences may have "pushed" Dolly Varden into a greater use of benthic space and food and cutthroat trout into greater use of limnetic resources in their respective allopatric lakes than might otherwise have occurred if these habitats had been more similar.

### Changes in Zooplankton Prey

Summer maximum densities of the two crustacean zooplankters most heavily preyed upon by cutthroat trout and Dolly Varden were similar in the three study lakes before fish transfers began (see fig. 3 of Northcote et al. 1978). During and immediately after fish introductions to the allopatric lakes there was either no change or an increase in densities of these zooplankters. On the other hand, the numbers of midwater third and fourth instar chaoborid larvae were reduced to such low levels that they were rarely caught by Clarke–Bumpus zooplankton sampling during the year after fish introductions were completed.

The maximum average body size of crustacean zooplankton prey during the summer–autumn period was much smaller in sympatric Loon Lake than in either of the allopatric lakes before fish introduction. After fish were introduced to the allopatric lakes the body size of both *Daphnia rosea* and *Diaptomus kenai* decreased significantly (see fig. 4 of Northcote et al. 1978).

Directly or indirectly, Dolly Varden and cutthroat trout introductions to the two formerly fishless lakes have had major effects on body size of their zooplanktonic prey populations. At first sight this might be taken to indicate strong size-selective predation by fish. However, *Bosmina longirostris*, a species rarely taken by Dolly Varden or cutthroat trout, significantly increased in body size at this time so that there may well have been effects from relaxation of invertebrate predation, particularly that of the two chaoborid species whose populations were virtually eliminated within a year after fish introductions. These invertebrates do have significant impacts on crustacean zooplankters within the study lakes (Fedorenko 1975a, 1975b; Neill 1981).

With continuing fish predation pressure, the size and perhaps abundance of preferred prey species may decrease, as has been documented in other lakes (Brooks 1968; Galbraith 1967). Both allopatric populations are reproducing in inlet streams to their lakes, and young fish without the possibility of sympatrically induced behavioural characteristics are being recruited to the predator populations. For these and other reasons, sympatric and allopatric fish and prey populations are being reexamined (e.g. see Jonsson et al. 1984).

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## References

ANDRUSAK, H., AND T. G. NORTHCOTE. 1970. Management implications of spatial distribution and feeding ecology of cutthroat trout and Dolly Varden in coastal British Columbia lakes. B.C. Fish Wildl. Branch, Fish. Manage. Publ. 13: 14 p.

1971. Segregation between adult cutthroat trout (*Salmo clarki*) and Dolly Varden (*Salvelinus malma*) in small coastal British Columbia lakes. J. Fish. Res. Board Can. 28: 1259–1268.

ARMITAGE, G. N. 1973. Character displacement and variability in lacustrine sympatric and allopatric Dolly Varden (*Salvelinus malma*) populations. M.Sc. thesis, Department of Zoology, University of British Columbia, Vancouver, B.C. 119 p.

BEAMISH, R. J. 1973. Design of a trapnet with interchangeable parts for the capture of large and small fishes from varying depths. J. Fish. Res. Board Can. 30: 587–590.

BRIAN, M.V. 1956. Segregation of species of the ant genus *Myrmica*. J. Anim. Ecol. 25: 319–337.

BROOKS, J. L. 1968. The effect of prey size selection by lake planktivores. Syst. Zool. 17: 272–291.

FEDORENKO, A. Y. 1975a. Instar and species-specific diets in two species of *Chaoborus*. Limnol. Oceanogr. 20: 238–249.

1975b. Feeding characteristics and predation impact of *Chaoborus* (Diptera, Chaoboridae) larvae in a small lake. Limnol. Oceanogr. 20: 250–258.

FEDORENKO, A. Y., AND M. C. SWIFT. 1972. Comparative biology of *Chaoborus americanus* and *Chaoborus trivittatus* in Eunice Lake, British Columbia. Limnol. Oceanogr. 17: 721–730.

GALBRAITH, M. G. JR. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. Trans. Am. Fish. Soc. 96: 1–10.

HUME, J. M. B. 1978. Planktivorous feeding and habitat utilization of sympatric and experimentally segregated populations of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden char (*Salvelinus malma*). M.Sc. thesis, Department of Zoology, University of British Columbia, Vancouver, B.C. 143 p.

JONSSON, B., K. HINDAR, AND T. G. NORTHCOTE. 1984. Optimal age at sexual maturity of sympatric and experimentally allopatric cutthroat trout and Dolly Varden char. Oecologia (Berl.) 61: 319–325.

NEILL, W. E. 1981. Impact of *Chaoborus* predation upon the structure and dynamics of a crustacean zooplankton community. Oecologia (Berl.) 48: 164–177.

NILSSON, N.-A. 1960. Seasonal fluctuations in the food segregation of trout, char and whitefish in 14 north-Swedish lakes. Fish. Board Swed. Rep. Inst. Freshw. Res. Drottningholm 41: 185–205.

1963. Interaction between trout and char in Scandinavia. Trans. Am. Fish. Soc. 92:276–285.

1967. Interactive segregation between fish species, p. 295–313. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

NILSSON, N.-A., AND T. G. NORTHCOTE. 1981. Rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) interactions in coastal British Columbia lakes. Can. J. Fish. Aquat. Sci. 38: 1228–1246.

NORTHCOTE, T. G., AND R. CLAROTTO. 1975. Limnetic macrozooplankton and fish predation in some coastal British Columbia lakes. Verh. Int. Ver. Limnol. 19: 2378–2393.

NORTHCOTE, T. G., C. J. WALTERS, AND J. M. B. HUME. 1978. Initial impacts of experimental fish introductions on the macrozooplankton of small oligotrophic lakes. Verh. Int. Ver. Limnol. 20: 2003–2012.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman and Company, San Francisco, CA. 859 p.

WERNER, E. E., AND D. J. HALL. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science (Wash., DC) 191: 404–406.

WINDELL, J. T. 1971. Food analysis and rate of digestion, p. 215–226. *In* W. E. Ricker [ed.] Methods for assessment of fish production in fresh waters. Int. Biol. Progr. Handb. No. 3. Blackwell Scientific Publications, Oxford.

# Natural Hybridization between Steelhead Trout (*Salmo gairdneri*) and Coastal Cutthroat Trout (*Salmo clarki clarki*) in Two Puget Sound Streams

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A genetic investigation of anadromous trout populations in the Puget Sound area revealed numerous juvenile individuals from two streams with electrophoretic phenotypes consistent with those expected for hybrid descendents of steelhead trout (*Salmo gairdneri*) and coastal cutthroat trout (*S. clarki clarki*). The likelihood of hybridization was evaluated with a hybrid index measuring the relative probability that the combined genotype for a particular fish at several diagnostic loci could have arisen by random mating within each of the two *Salmo* species. The distribution of hybrid index scores among fish from the two creeks clearly demonstrated the genetic distinctness of the two species and the intermediate genotypic composition of the unknown fish. We concluded that these electrophoretically intermediate fish were natural steelhead–cutthroat hybrids based on their restricted occurrence at specific sample sites in only 2 of 23 streams surveyed, the linear distributions of juveniles from the two parental species within each stream, and the distribution of hybrid index values for a hatchery population of known mixed ancestry. Further, from estimates of gametic disequilibria and the absence of a consistent excess of heterozygotes we suggest that backcrossing may have occurred. The existence of these natural hybrids raises many questions concerning the biological bases for maintaining species integrities in regions of sympatry and indicates the need to fully understand the biological consequences of present and future management practices.

L'étude des caractères génétiques des populations de truites anadromes de la baie Puget a révélé que dans deux ruisseaux se jetant dans cette baie, il y a de nombreux poissons juvéniles dont les propriétés phénotypiques, déterminées par électrophorèse, correspondent à celles qu'on trouverait chez l'hybride de la truite steelhead (*Salmo gairdneri*) et de la truite fardée (*S. clarki clarki*) des eaux côtières. Nous avons déterminé la vraisemblance d'une telle hybridation au moyen d'un indice exprimant la probabilité relative que le génotype mixte d'un poissons donné, analysé en plusieurs loci, se manifeste à la suite d'accouplements déterminés au hasard chez chacune des deux espèces. La distribution des valeurs de l'indice d'hybridation des poissons des deux ruisseaux montre clairement que les deux espèces sont génétiquement distinctes et que la composition du génotype du poisson inconnu est de type intermédiaire. Nous avons conclu que le poisson présentant des propriétés électrophorétiques intermédiaires est un hybride naturel produit par le croisement de la truite steelhead et de la truite fardée, compte tenu du fait que nous n'en avons trouvé qu'à certains postes d'échantillonnage dans seulement 2 des 23 cours d'eau étudiés, et étant donné la distribution des juvéniles des deux espèces parentales dans chacun des cours d'eau et la distribution des valeurs de l'indice d'hybridation d'une population d'élevage de généalogie connue. De plus, d'après l'estimation du déséquilibre gamétique et étant donné l'absence d'un surplus constant d'hétérozygotes, nous pensons qu'il aurait pu y avoir croisement en retour. L'existence de ces hybrides non seulement soulève de nombreuses questions au sujet des principes de biologie qui gouvernent l'intégrité des espèces sympatriques, mais montre aussi qu'il est important de bien connaître les conséquences des mesures d'aménagement.

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Congeneric species of fish often hybridize in nature (Hubbs 1955; Schwartz 1972) and numerous examples of this phenomenon have been documented for the genus *Salmo* (Payne et al. 1972; Soloman and Child 1978; Beland et al. 1981; Schreck and Behnke 1971; Behnke 1979; references in Dangel et al. 1973). The interbreeding of introduced rainbow trout (*S. gairdneri*) and inland forms of cutthroat trout (*S. clarki* ssp.) native to the western United States has further resulted in extensive introgression and hybrid swarms, thereby destroying the genetic integrities of the native populations (Behnke and Zarn 1976; Behnke 1979; Allendorf and Phelps 1981; Busack and Gall 1981).

Anadromous forms of coastal cutthroat trout (*S. clarki clarki*) and rainbow trout (i.e. steelhead trout) naturally coexist sympatrically along the west coast of North America; however, natural hybridization between these two taxa has never been formally documented. Several investigators have noted juvenile trout with external appearances intermediate to the two *Salmo* species (DeWitt 1954; Needham and Gard 1959; Hartman and Gill 1968) but no definitive statements were made regarding hybrid status. In general, the existence of morphologically intermediate fish cannot be interpreted as proof that natural hybridization has occurred because the extent of intraspecific phenotypic variation is usually unknown and hybrids are not always morphologically intermediate to the parental species (Neff and Smith 1979; Ross and Cavender 1981; Leary et al. 1983). Identifying potential hybrids of *S. gairdneri* and *S. clarki clarki* in coastal streams of western North America is further complicated because adults of both species reside in salt water and juveniles are very difficult to distinguish morphologically under field conditions (Crawford 1925; Dymond 1928; Miller 1950; McConnell and Snyder 1972).

In recent years, protein electrophoresis has been shown to be a powerful technique for identifying hybrid fish (e.g.Nyman 1970; Reinitz 1977; Danzmann and Down 1982). The technique has proven particularly valuable for detecting natural hybridization between inland forms of cutthroat trout and non-native rainbow trout (Allendorf and Phelps 1981; Busack and Gall 1981).

In this paper, we document the existence of natural hybrids of *S. gairdneri* and *S. clarki clarki* in two Puget Sound streams using electrophoretic data. We consider then the biological and management implications of our findings.

## Materials and Methods

### Sampled Populations

Electrophoretic differences between *S. gairdneri* and *S. clarki clarki* were identified by examining several hatchery populations of both species. The following populations, all maintained by the Washington State Department of Game (Crawford 1979), were sampled for this study (abbreviations and sample sizes in parentheses).

*Salmo clarki clarki*: Beaver Creek cutthroat trout (*CTBC*, $n = 100$), Cowlitz River cutthroat trout (*CTCR*, $n = 200$), Hood Canal cutthroat trout (*CTHC*, $n = 286$), Stillaguamish River cutthroat trout (*CTSR*, $n = 98$), and Tokul Creek cutthroat trout (*CTTC*, $n = 97$);

*Salmo gairdneri*: Chambers Creek steelhead trout (*SHCC*, $n = 96$), Washougal River steelhead trout (*SHWR*, $n = 95$), Goldendale rainbow trout (*RBGD*, $n = 49$), and South Tacoma rainbow trout (*RBST*, $n = 30$).

Two of the four *gairdneri* populations are resident rainbow trout (*RBGD* and *RBST*) and the other two populations are anadromous steelhead trout (*SHCC* and *SHWR*). The Tokul Creek population (*CTTC*) is the only resident population of cutthroat trout; the other four populations are anadromous. The Beaver Creek population (*CTBC*) was specifically sampled for this study because of suspected introgressive hybridization with steelhead trout (Crawford 1979). Previous electrophoretic analyses of both species provided further information on intraspecific genetic variation (Allendorf 1975; Campton 1981).

Juvenile trout were collected from 23 streams in the Puget Sound area during September and October 1977 (Campton 1981). Of these 23 streams, electrophoretic phenotypes for fish from the following 2 streams are described here: (1) Harvey Creek, a tributary of the Stillaguamish River near Arlington, WA, and (2) Big Mission Creek, a tributary to the southern arm of Hood Canal near Belfair, WA. Separate samples totaling 450 fish were collected from four sites within Harvey Creek; these sites were 1.9, 2.4, 2.9, and 3.2 km upstream from the stream's confluence with the Stillaguamish River and are respectively called sites 1, 2, 3, and 4. A total of 262 fish were collected from three sites within Big Mission Creek; these sites were 0.8, 5.4, and 8.8 km upstream from the stream's terminus on southern Hood Canal and are respectively called sites 1, 2, and 3. Individuals were not identified according to species prior to being electrophoretically examined, although both *gairdneri* and *clarki* were thought to be present based on external morphological characteristics (McConnell and Snyder 1972). All fish were less than 150 mm in length (FL) and were believed to be presmolt juveniles representing anadromous populations. Scales were taken from subsamples of fish to determine age–length relationships at each sample site. Samples were frozen in the field using dry ice and subsequently stored at −25°C for up to 6 mo prior to electrophoretic analysis.

### Electrophoresis

Horizontal starch–gel electrophoresis followed the general procedures of Utter et al. (1974) and May et al. (1979). Starch gels were prepared with a 13% mixture of Electrostarch (Electrostarch Company; Madison, WI) and one of four (I, II, III, or IV) gel buffer solutions. Buffers referred to as systems I, II, and III here were described by Ridgway et al. (1970), Markert and Faulhaber (1965), and Clayton and Tretiak (1972), respectively. A fourth buffer system (system IV) was devised by combining the gel buffer of Clayton and Tretiak (1972) with electrode buffer No. I from Shaw and Prasad (1970). Loci and alleles were designated according to the nomenclature system proposed by Allendorf and Utter (1979). The common *S. gairdneri* allele was assigned a standard mobility of *100*, and *S.c. clarki* alleles as well as variant *gairdneri* alleles were measured anodically relative to this standard. Tissue specificity of enzyme and locus expression for salmonid fishes has previously been described (Utter et al. 1980).

The following enzymes (EC number, resolving buffer systems and loci in parentheses) were examined in muscle, liver, or eye tissue homogenates: aspartate aminotransferase (2.6.1.1; I, II; *AAT-1,2,3*), alcohol dehydrogenase (1.1.1.1; I; *ADH*), creatine kinase (2.7.3.2; I; *CK-1,2*), glucosephosphate isomerase (5.3.1.9; I; *GPI-1,2,3*), glycerol-3-phosphate dehydrogenase (1.1.1.8; IV; *G3PDH-1,2*), glycyl-leucine dipeptidase (3.4.13.11; II; *GLD-1,2*), isocitrate dehydrogenase (1.1.1.42; III; *IDH-1,2,3,4*), lactate dehydrogenase (1.1.1.27;

TABLE 1. Allele frequencies at species-discriminating loci for hatchery populations of *S. gairdneri* and *S. clarki clarki*. The Beaver Creek population of coastal cutthroat trout (*CTBC*) is believed to be an introgressed population of steelhead–cutthroat hybrids (Crawford 1979). Average allele frequencies for the two species were calculated as the unweighted (by sample size) arithmetic averages of the allele frequencies for the respective hatchery populations, excluding *CTBC* from the calculations for *S. clarki clarki*. ND = no data.

| | | *S. gairdneri* | | | | | | *S. clarki clarki* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Loci | Alleles | *RBGD* | *RBST* | *SHWR* | *SHCC* | Avg. | *CTBC* | *CTCR* | *CTHC* | *CTSR* | *CTTC* | Avg. |
| *GLD-1* | *120* | — | — | — | — | — | — | — | 0.068 | — | — | 0.017 |
| | *110* | — | 0.050 | 0.031 | — | 0.020 | 0.550 | 0.968 | 0.777 | 0.964 | 0.865 | 0.894 |
| | *100* | 1.000 | 0.950 | 0.844 | 1.000 | 0.949 | 0.450 | 0.032 | 0.155 | 0.036 | 0.135 | 0.090 |
| | *90* | — | — | 0.125 | — | 0.031 | — | — | — | — | — | — |
| *IDH-3,4* | *124* | — | 0.042 | 0.016 | 0.043 | 0.025 | — | 0.037 | 0.007 | — | — | 0.011 |
| | *100* | 0.897 | 0.641 | 0.637 | 0.750 | 0.731 | 0.425 | 0.198 | 0.106 | 0.131 | 0.024 | 0.115 |
| | *72*[a] | 0.026 | 0.033 | 0.171 | 0.105 | 0.084 | 0.386 | 0.754 | 0.639 | 0.815 | 0.976 | 0.796 |
| | *44* | 0.077 | 0.267 | 0.168 | 0.102 | 0.154 | 0.189 | 0.011 | 0.248 | 0.054 | — | 0.078 |
| | *38* | — | 0.017 | 0.008 | — | 0.006 | — | — | — | — | — | — |
| *ME-4* | *110* | — | 0.067 | — | — | 0.017 | ND | ND | 1.000 | 1.000 | 0.916 | 0.972 |
| | *100* | 1.000 | 0.933 | 1.000 | 1.000 | 0.983 | | | — | — | 0.084 | 0.028 |
| *SDH-1* | *230* | — | — | — | — | — | — | 0.002 | — | — | — | 0.001 |
| | *190* | — | — | — | — | — | 0.294 | 0.828 | 0.889 | 0.916 | 0.964 | 0.899 |
| | *100* | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.706 | 0.170 | 0.111 | 0.084 | 0.036 | 0.100 |

[a]The *72* allele in *clarki* consists of three electromorphs, *65*, *72*, and *80*, which are difficult to distinguish electrophoretically. The *65* and *80* alleles were not observed in *S. gairdneri*.

I, II; *LDH-1,2,3,4,5*), malate dehydrogenase (1.1.1.37; III, IV; *MDH-1,2,3,4*), malic enzyme (1.1.1.40; III, IV; *ME-1,2,3,4*), mannosephosphate isomerase (5.3.1.8; II; *MPI*), phosphoglucomutase (2.7.5.1; I; *PGM*), phosphogluconate dehydrogenase (1.1.1.44; IV; *PGD*), sorbitol dehydrogenase (1.1.1.14; I; *SDH-1,2*), and superoxide dismutase (1.15.1.1; I; *SOD*). Staining methods followed standard procedures and have been extensively described elsewhere (e.g. Shaw and Prasad 1970; Harris and Hopkinson 1976; Allendorf et al. 1977).

Several isozyme systems in salmonid fishes are represented by duplicated loci with common allelic forms of identical electrophoretic mobilities (Allendorf et al. 1975; May et al. 1979). These duplicated loci (*AAT-1,2*; *IDH-3,4*; *MDH-1,2*; *MDH-3,4*; *ME-1,2*) were treated as two disomic loci with identical allele frequencies because allelic variation could not be attributed to a specific locus.

### Statistics

Goodness of fit to Hardy–Weinberg proportions was tested for significance using the likelihood-ratio test or *G*-statistic (Sokal and Rohlf 1969). Gametic (linkage) disequilibria among loci were estimated by Burrow's composite measure (Weir 1979), which does not require the assumption of a random mating population in Hardy–Weinberg proportions. Disequilibria were tested for significance using the statistic $Nr^2$ where $r$ is the estimated correlation between alleles, properly adjusted for departures from Hardy–Weinberg proportions, and $N$ is the sample size (Weir 1979).

In order to fully assess the likelihood of hybridization between *S. gairdneri* and *S. clarki clarki*, we have derived a hybrid index that measures the relative probability that the combined genotype for a particular fish at several loci could have arisen by random mating from within each of the two *Salmo* species (see Appendix for derivation). The index can assume values from zero (0.0) to one (1.0) where values close to 0.0 or 1.0 indicate that the individual has a very high relative probability of being a cutthroat trout (*clarki*) or steelhead trout (*gairdneri*), respectively. Substantial numbers of individuals with scores near 0.5 would therefore provide strong evidence for hybridization. The index is based on the average allele frequencies presented in this paper for the hatchery populations of the two species (see Appendix for details).

## Results

Rainbow (steelhead) trout and coastal cutthroat trout expressed different common alleles at the following loci: *CK-2*, *GLD-1*, *IDH-3,4*, *ME-4*, and *SDH-1*. The four hatchery populations of *S. gairdneri* appeared fixed for the *100* and *114* alleles at *CK-1* and *CK-2*, respectively, whereas the hatchery populations of *S. clarki clarki* (excluding *CTBC*) appeared monomorphic for the *100* allele at both loci. Phenotypes at *CK-1,2* were not used to characterize putative hybrids, however, because of difficulties in distinguishing two- and three-banded phenotypes (see Utter et al. 1979 for details of CK expression). The other four distinguishing isozyme systems were clearly expressed in the two species and were therefore used to distinguish *S. gairdneri* and *S. clarki clarki* in the wild population samples. Each of these systems was polymorphic in one or more hatchery populations, and average allele frequencies at these loci for the two species (Table 1) were used as input parameters for the hybrid index function (Appendix). All other loci were characterized by common alleles of identical electrophoretic mobility in the two species.

Electrophoretic phenotypes for the Beaver Creek population (*CTBC*) confirmed earlier suspicions (Crawford 1979) regarding a hybrid ancestry for this hatchery population (Table 1; Fig. 1). Allele frequencies for *CTBC* at the diagnostic loci were intermediate to the averages for the other hatchery populations of *clarki* and *gairdneri* (Table 1), and the distribution of hybrid index values closely resembled a normal distribution (Fig. 1). This population also appeared to be polymorphic for two- and

TABLE 2. Observed numbers of fish from Big Mission Creek expressing each genotype at the diagnostic loci. Age 0+ fish from site 3 expressed composite genotypes suggestive of a mixed *clarki–gairdneri* ancestry and could not be separated according to species. *G*-statistics (Sokal and Rohlf 1969) measure goodness of fit to Hardy–Weinberg proportions. Only allele frequencies are listed for *IDH-3,4*. $^{**}P < 0.01$; $^{***}P < 0.001$.

| Genotype | Site 1, 0+ (SH) | Site 2 | | | Site 3 | |
|---|---|---|---|---|---|---|
| | | 0+ (SH) | 0+ (CT) | 1+ (CT) | 0+ (Unk.) | 1+ (CT) |
| *GLD-1* | | | | | | |
| *100/100* | 36 | 54 | 1 | 2 | 3 | — |
| *100/110* | — | — | 3 | 4 | 76 | 6 |
| *110/110* | — | — | 12 | 20 | 10 | 22 |
| *100/120* | — | — | — | 1 | 9 | — |
| *110/120* | — | — | — | 1 | 1 | — |
| *G*-statistic | — | — | 1.09 | 4.69 | 61.0*** | 0.72 |
| *ME-4* | | | | | | |
| *100/100* | 36 | 54 | — | — | 29 | — |
| *100/110* | — | — | 2 | 2 | 50 | — |
| *110/110* | — | — | 14 | 27 | 13 | 28 |
| *G*-statistic | — | — | 0.13 | 0.07 | 1.36 | — |
| *SDH-1* | | | | | | |
| *100/100* | 36 | 54 | 1 | 3 | 13 | 1 |
| *100/190* | — | — | 5 | 9 | 26 | 8 |
| *190/190* | — | — | 10 | 17 | 49 | 19 |
| *G*-statistic | — | — | 0.11 | 1.00 | 7.10** | 0.02 |
| *IDH-3,4* | | | | | | |
| *124* | 0.014 | 0.005 | — | — | — | — |
| *100* | 0.707 | 0.923 | — | 0.036 | 0.448 | 0.071 |
| *72* | 0.221 | 0.056 | 1.000 | 0.955 | 0.552 | 0.920 |
| *44* | 0.057 | 0.015 | — | 0.009 | — | 0.009 |
| *N* | 35 | 49 | 16 | 28 | 87 | 28 |

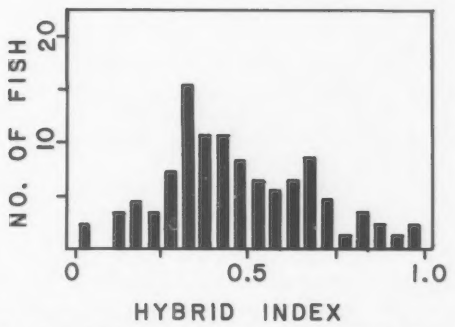


FIG. 1. Distribution of hybrid index scores ($I_H$) for the Beaver Creek hatchery population (*CTBC*). Index scores close to 1.0 or 0.0 indicate a very high probability that the individual is either a steelhead trout or a cutthroat trout, respectively. The Beaver Creek population is believed to be an introgressed population of steelhead–cutthroat hybrids (Crawford 1979).

three-banded phenotypes at *CK-1,2* but fish were not individually scored at these loci. Genotypes for *CTBC* conformed to Hardy–Weinberg proportions at all other scored loci ($P > 0.05$).

Substantial numbers of age 0+ fish from site 3 of Big Mission Creek and sites 1 and 2 of Harvey Creek expressed electrophoretic phenotypes suggestive of a mixed steelhead–cutthroat ancestry (Tables 2 and 3). Age 0+ fish from all other sample sites were easily identified electrophoretically as either steelhead trout or as cutthroat trout, and all age 1+ fish were identified as cutthroat trout. The observed numbers of fish expressing each genotype at the diagnostic loci are tabulated by sample site, age-class, and species in Tables 2 and 3. Samples of age 0+ fish containing putative hybrids have not been separated according to species, and genotypes are reported collectively. Only allele frequencies are given for *IDH-3,4* because of the large number of possible genotypes at this duplicated locus and the inability to test for Hardy–Weinberg proportions.

Only those samples containing putative hybrids expressed significant deviations from random mating proportions (Tables 2 and 3). Age 0+ fish from site 3 of Big Mission Creek collectively expressed an excess of heterozygotes at *GLD-1* ($P < 0.001$) and a deficit of heterozygotes at *SDH-1* ($P < 0.01$) whereas age 0+ fish from sites 1 and 2 of Harvey Creek expressed a deficit of heterozygotes at both *ME-4* and *SDH-1* ($P < 0.001$).

The distribution of hybrid index scores supported the hypothesis that young-of-the-year hybrids were present at site 3 of Big Mission Creek and sites 1 and 2 of Harvey Creek (Fig. 2 and 3). All age 0+ fish from sites 1 and 2 of Big Mission Creek expressed very high relative probabilities of either being a cutthroat trout or a steelhead trout (Fig. 2a, 2b), whereas index values for age 0+ fish from site 3 resembled a normal distribution (Fig. 2e). Index values for several age 0+ individuals from site 3 were less than 0.05, suggesting that some "pure" cutthroat trout were also present. Similarly, index values for age 0+ fish from sites 1 and 2 of Harvey Creek ranged almost continuously from 0.0 to 0.95 (Fig. 3a, 3c) whereas the distribution of hybrid index values for age 0+ fish from sites 3 and 4 were highly skewed towards zero (Fig. 3e, 3g). Index scores for age 0+ fish from sites 1 and 2 of Harvey Creek did not resemble a normal distribution, as did scores for age 0+ fish

TABLE 3. Observed number of fish from Harvey Creek expressing each genotype at the diagnostic loci. Age 0+ fish from sites 1 and 2 expressed composite genotypes suggestive of a mixed *clarki–gairdneri* ancestry and could not be separated according to species. *G*-statistics (Sokal and Rohlf 1969) measure goodness of fit to Hardy–Weinberg proportions. Only allele frequencies are listed for *IDH-3,4*. $^{**}P < 0.01$; $^{***}P < 0.001$.

| | Site 1 | | Site 2 | | Site 3 | | Site 4 | |
|---|---|---|---|---|---|---|---|---|
| Genotype | 0+ (Unk.) | 1+ (CT) | 0+ (Unk.) | 1+ (CT) | 0+ (CT) | 1+ (CT) | 0+ (CT) | 1+ (CT) |
| *GLD-1* | | | | | | | | |
| *100/100* | 4 | — | 5 | — | — | — | — | — |
| *100/110* | 26 | 1 | 19 | 3 | 7 | 5 | 7 | 2 |
| *110/110* | 24 | 45 | 36 | 32 | 38 | 34 | 78 | 46 |
| *100/120* | 1 | — | 2 | — | — | — | — | — |
| *110/120* | 2 | 2 | 6 | 3 | 3 | 3 | — | 12 |
| *120/120* | 1 | — | — | — | — | — | — | — |
| *G*-statistic | 4.21 | 0.10 | 1.56 | 0.52 | 1.17 | 0.84 | 0.30 | 1.86 |
| *ME-4* | | | | | | | | |
| *100/100* | 9 | — | 11 | — | — | — | — | — |
| *100/110* | 12 | 2 | 9 | — | — | — | — | — |
| *110/110* | 36 | 45 | 47 | 38 | 51 | 42 | 35 | 60 |
| *G*-statistic | 11.1*** | 0.04 | 23.2*** | — | — | — | — | — |
| *SDH-1* | | | | | | | | |
| *100/100* | 10 | 2 | 6 | 2 | — | 1 | — | — |
| *100/190* | 10 | 4 | 11 | 5 | — | — | 2 | — |
| *190/190* | 38 | 41 | 51 | 31 | 51 | 41 | 82 | 60 |
| *190/230* | — | — | — | — | — | — | 1 | — |
| *G*-statistic | 16.3*** | 5.64[a] | 9.82** | 3.68 | — | 9.45[a] | 0.05 | — |
| *IDH-3,4* | | | | | | | | |
| *100* | 0.422 | — | 0.329 | — | 0.141 | 0.138 | 0.084 | 0.066 |
| *72* | 0.456 | 0.826 | 0.579 | — | 0.724 | 0.713 | 0.843 | 0.878 |
| *44* | 0.123 | 0.174 | 0.091 | — | 0.135 | 0.150 | 0.072 | 0.056 |
| *N* | 51 | 46 | 63 | 0 | 48 | 40 | 83 | 49 |

[a]*G*-statistic values are inflated for these comparisons because the expected number of some genotypes is less than 1.0.

from site 3 of Big Mission Creek (Fig. 2e), but instead appeared to reflect three distinct groups of fish with different mean values (Fig. 3a and 3c). In contrast, all age 1+ fish from Big Mission and Harvey Creeks expressed hybrid index values conforming to those expected for cutthroat trout (i.e. highly skewed towards zero; Fig. 2c, 2d; 3b, 3d, 3f, 3h) except for one individual from site 2 of Big Mission Creek (Fig. 2c). This individual's composite genotype was *GLD-1(100/100)*, *ME-4(110/110)*, and *SDH-1(100/100)*, suggesting it may have been a rare cutthroat trout that was homozygous for the common *gairdneri* allele at two distinguishing loci *(GLD-1* and *SDH-1)* or a backcross progeny between an F1 hybrid and a cutthroat trout (the genotype of this fish at *IDH-3,4* could not be scored). Age 0+ steelhead trout and age 0+ cutthroat trout were both present at site 2 of Big Mission Creek but were clearly distinguished electrophoretically by their hybrid index scores (Fig. 2b).

In order to evaluate the possibility of backcrossing and introgression between *S. gairdneri* and *S. clarki clarki* in the two creeks, we have estimated the amount of gametic (linkage) disequilibrium among *GLD-1*, *ME-4*, and *SDH-1* for each of the species groups listed in Tables 2 and 3. Estimates of disequilibrium were significantly different from zero at all pairwise combinations of loci for the three groups of age 0+ fish in which putative hybrids were found (Table 4). These estimates were all greater than zero ($D > 0$), reflecting a positive correlation among common alleles from the same species. However, estimates of disequilibrium would be inflated in a positive direction if individuals of both parental species were present, as suggested by Fig. 3a and 3c for Harvey Creek. Disequilibrium estimates for age 0+ cutthroat trout and steelhead trout from all other sample sites and for age 1+ cutthroat trout from all sample sites were not significantly different from zero.

We have partitioned each of the samples of age 0+ fish containing putative hybrids into three subgroups based on hybrid index scores; fish with index scores less than 0.30, greater than 0.80, and between the two values have been provisionally classified as "cutthroat trout" (CT), "steelhead trout" (CT), and "hybrids" (HB), respectively (see Fig. 2 and 3). These classifications result in two groups of age 0+ fish (CT and HB) from site 3 of Big Mission Creek and three groups of age 0+ fish (CT, HB, and SH) from sites 1 and 2 of Harvey Creek, where fish from sites 1 and 2 of Harvey Creek have been pooled (Table 5). Fish classified as steelhead trout and cutthroat trout from Harvey Creek both conformed to Hardy–Weinberg proportions at all three loci (*GLD-1*, *ME-4*, and *SDH-1*) whereas fish classified as hybrids were composed of a large excess of heterozygotes at the *GLD-1* locus only ($P < 0.001$). Age 0+ fish partitioned as cutthroat trout and hybrids from site 3 of Big Mission Creek both expressed significant excesses of heterozygotes at *GLD-1* and *ME-4* but no significant deviations from Hardy–Weinberg proportions at *SDH-1*. Estimates of gametic disequilibrium among the diagnostic loci were not significant for any of the species subgroups from Harvey Creek or for fish classified as hybrids from Big Mission Creek but were significant between the *GLD-1* and *ME-4* loci for age 0+ fish classi-

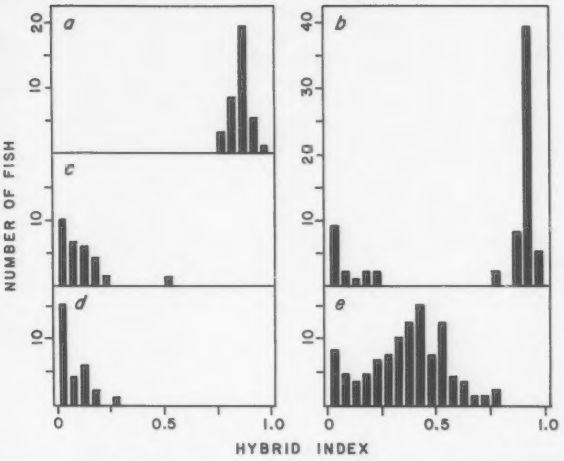


FIG. 2. Distribution of hybrid index scores for trout collected from Big Mission Creek. (a) Age 0+ fish, site 1; (b) age 0+ fish, site 2; (c) age 1+ fish, site 2; (d) age 1+ fish, site 3; (e) age 0+ fish, site 3. Sites 1, 2, and 3 are 0.8, 5.4, and 8.8 km upstream from the creek's terminus.

fied as cutthroat trout from site 3 of Big Mission Creek (Table 6). The data in Tables 5 and 6 are therefore consistent with the hypothesis that three distinct types of fish were found at sites 1 and 2 of Harvey Creek: cutthroat trout, steelhead trout, and 35 age 0+ fish of mixed origin. The absence of any significant disequilibria for these 35 "hybrid" fish suggests that they were not strictly F1 hybrids; in fact, the estimated correlation between alleles at *ME-4* and *SDH-1* was negative ($r = -0.263$) although nonsignificant ($P > 0.05$). On the other hand, nonrandom associations among alleles, both within and between loci, for age 0+ fish classified as cutthroat trout from site 3 of Big Mission Creek indicate that these fish cannot be legitimately separated from the other fish classified as hybrids (see Fig. 2e).

## Discussion

The data presented in Tables 1–6 and the distribution of hybrid index scores in Fig. 2 and 3 provide convincing evidence that natural hybridization between *S. gairdneri* and *S. clarki clarki* has occurred in two Puget Sound streams. One must recognize, however, that the presence of fish with intermediate phenotypes, whether morphologic or electrophoretic, can never constitute actual proof of hybridization. Nevertheless, we believe hybridization is the only plausible explanation for the relatively high numbers of fish with intermediate phenotypes from the two streams given the distribution of index scores for a hatchery population of known hybrid ancestry (*CTBC*; Fig. 1) and the knowledge that electrophoretic markers are direct gene products. One can never exclude intraspecific genetic variation within *S. clarki clarki* as the source of the intermediate phenotypes but the probability of producing such relatively large numbers of electrophoretically intermediate fish at two separate locations by random mating within *clarki* alone is extremely remote.

The extent of backcrossing and introgression resulting from natural hybridization between *S. gairdneri* and *S. clarki clarki* is difficult to ascertain. One or both of the parental species are naturally polymorphic at the four distinguishing isozyme systems, and backcross or F2 progeny cannot, therefore, be individually distinguished from F1 hybrids. If the fish we classified as hybrids (using hybrid index scores) had expressed a large excess of heterozygotes at *GLD-1*, *ME-4*, and *SDH-1*, then one could safely conclude that only F1 hybrids had been sampled. However, an excess of heterozygotes was not consistently observed (Table 5). More importantly, however, age 0+ fish classified as cutthroat trout from site 3 of Big Mission Creek expressed an excess of heterozygotes at *GLD-1* and *ME-4* (Table 5) as well as a positive correlation between alleles at these two loci (Table 6). These results are suggestive of backcrossing between F1 hybrids and cutthroat trout in Big Mission Creek. The data are not as clear-cut for age 0+ fish from Harvey Creek but descendents of an F1 mating are also suggested (Tables 5 and 6). We cannot, therefore, exclude the possibility that some (or all) of the putative hybrids were backcross or F2 progeny. Nevertheless, the preferential expression of maternal or paternal isozymes in trout hybrids is not uncommon (e.g. Hitzeroth et al. 1968; Ohno 1969; Engel et al. 1977) and this phenomenon could produce F1 hybrid pheno-

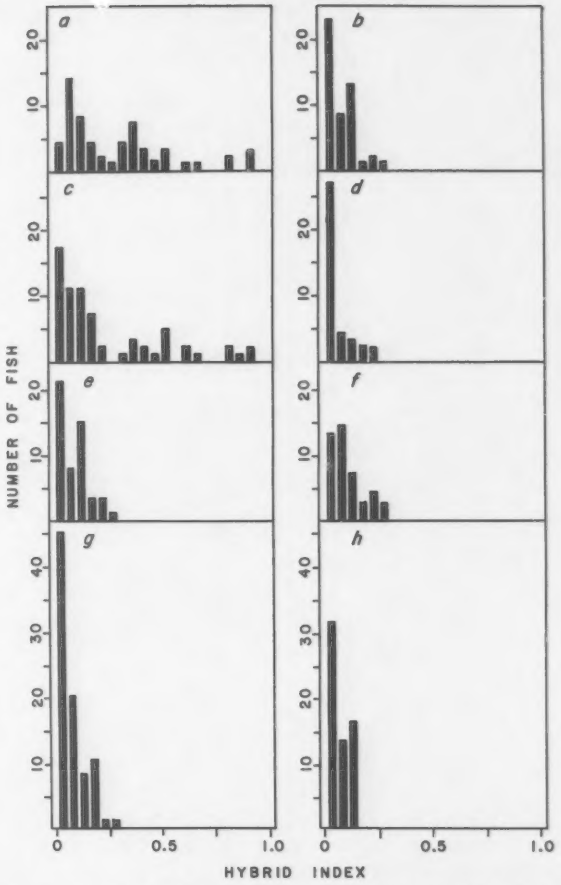


FIG. 3. Distribution of hybrid index scores for trout collected from Harvey Creek. (a) Age 0+ fish, site 1; (b) age 1+ fish, site 1; (c) age 0+ fish, site 2; (d) age 1+ fish, site 2; (e) age 0+ fish, site 3; (f) age 1+ fish, site 3; (g) age 0+ fish, site 4; (h) age 1+ fish, site 4. Sites 1, 2, 3, and 4 are 1.9, 2.4, 2.9, and 3.2 km upstream from the confluence of this creek with the Stillaguamish River.

TABLE 4. Estimates of gametic (linkage) disequilibrium for each of the sample groups listed in Tables 2 and 3. Loci 1, 2, and 3 refer to *GLD-1*, *ME-4*, and *SDH-1*, respectively. $D$ is Burrow's composite measure of gametic disequilibrium, $D'$ is the proportion of the maximum possible disequilibrium given the estimated allele frequencies, $R$ is the correlation between alleles at different loci appropriately adjusted for departures from Hardy–Weinberg proportions, and $\chi^2$ is the goodness of fit statistic ($= NR^2$) with 1 df for testing $H_0$: $D = 0$ (see Weir 1979 for details). Loci were made diallelic by pooling all alleles except the common *gairdneri* allele (allele *100*). $*P < 0.05$; $***P < 0.001$.

| Site, species, age | Loci | $D \pm$ SE | $D'$ | $R$ | $\chi^2$ |
|---|---|---|---|---|---|
| Big Mission Creek | | | | | |
| Site 2, CT, 0+ | (1,2) | 0.013±0.029 | 0.237 | 0.122 | 0.23 |
| | (1,3) | 0.060±0.053 | 0.495 | 0.319 | 1.63 |
| | (2,3) | 0.038±0.035 | 0.768 | 0.349 | 1.95 |
| Site 2, CT, 1+ | (1,2) | −0.012±0.010 | 0.397 | −0.148 | 0.62 |
| | (1,3) | 0.046±0.043 | 0.384 | 0.218 | 1.33 |
| | (2,3) | −0.019±0.011 | 0.723 | −0.208 | 1.26 |
| Site 3, Unk., 0+ | (1,2) | 0.026±0.011 | 0.131 | 0.239 | 5.26* |
| | (1,3) | 0.033±0.016 | 0.204 | 0.229 | 4.60* |
| | (2,3) | 0.062±0.027 | 0.500 | 0.248 | 5.09* |
| Site 3, CT, 1+ | (1,3) | 0.016±0.025 | 0.181 | 0.136 | 0.52 |
| Harvey Creek | | | | | |
| Site 1, Unk., 0+ | (1,2) | 0.153±0.035 | 0.827 | 0.647 | 23.8*** |
| | (1,3) | 0.157±0.035 | 0.869 | 0.652 | 24.6*** |
| | (2,3) | 0.154±0.043 | 0.793 | 0.519 | 15.3*** |
| Site 1, CT, 1+ | (1,3) | −0.002±0.003 | 0.196 | −0.053 | 0.13 |
| | (2,3) | −0.004±0.005 | 0.197 | −0.077 | 0.27 |
| Site 2, Unk., 0+ | (1,2) | 0.206±0.036 | >1.000 | 0.846 | 48.0*** |
| | (1,3) | 0.153±0.032 | >1.000 | 0.759 | 39.1*** |
| | (2,3) | 0.207±0.038 | >1.000 | 0.845 | 47.9*** |
| Site 2, CT, 1+ | (1,3) | 0.017±0.017 | 0.500 | 0.235 | 2.10 |
| Site 3, CT, 1+ | (1,3) | −0.003±0.006 | 0.130 | −0.057 | 0.14 |
| Site 4, CT, 0+ | (1,3) | −0.002±0.001 | 0.089 | −0.057 | 0.28 |

types suggestive of a backcross or F1 mating. Detailed experimental matings between the two species are required to resolve these questions.

The mechanisms preventing widespread hybridization between *S. gairdneri* and *S. clarki clarki* are not well understood. The ability of these two closely related species to coexist sympatrically and yet maintain their species integrities has generally been attributed to the spatial and temporal separation of spawning adults and not to a genetic incompatibility between species or other postzygotic isolating mechanism (Needham and Gard 1959; Behnke 1972, 1979). In western Washington, coastal cutthroat trout spawn between January and March whereas peak spawning for steelhead trout typically occurs between March and May (Johnston and Mercer 1976; Phillips et al. 1980). These two species also tend to segregate according to stream size and profile; cutthroat trout usually spawn in small, low-gradient creeks or in the upper low-flow reaches of large creeks whereas steelhead trout usually spawn in larger, swifter flowing streams (Hartman and Gill 1968; see also Fig. 2). Nevertheless, the time and place of spawning for the two species overlap considerably in a large number of tributary creeks in the Puget Sound area (Washington State Department of Game, unpubl. data). Olfactory recognition of conspecific fish during spawning (Liley 1982) may therefore provide a mechanism for the ethological isolation of spawning adults in areas of spatial and temporal sympatry. Differences in chromosome numbers between the two species (Gold et al. 1977; Thorgaard 1983) may provide an additional postzygotic isolating mechanism through reduced fertility and/or viability although the successful propagation of the Beaver Creek population would argue against a major genetic incompatibility. Major chromosomal differences among rainbow trout and subspecies of cutthroat trout can be attributed solely to centric fissions and fusions (Gold et al. 1977; Loudenslager and Thorgaard 1979; Thorgaard 1983), and meiotic pairing and assortment of homeologous chromosomes in F1 hybrids is apparently successful as evidenced by the existence of introgressed hybrid populations (Allendorf and Phelps 1981; Busack and Gall 1981).

The existence of numerous young-of-the-year hybrids of *S. gairdneri* and *S. clarki clarki* raises many questions as to why adult hybrids have not been previously reported. As sea-run adults, these two species are easily distinguished by obvious differences in size, shape, coloration, and overall physical appearance. One would expect F1 hybrid adults to be readily identifiable by some combination of unique intermediate characteristics. It is possible that hybrid adults appear morphologically very similar to one of the two parental species. First-generation hybrids of pink and chum salmon (*Oncorhynchus gorbuscha* and *O. keta*, respectively) retain much of the distinctive mottling coloration of their chum salmon parent and could easily be mistaken as a "pure" chum salmon by an unsuspecting observer (see plate 1, Simon and Noble 1968). Although steelhead–cutthroat hybrids are easy to produce artificially, formal physical descriptions of juvenile and adult hybrids are lacking. Nevertheless, many fishery biologists in Washington state have occasionally observed sea-run adults with physical characteristics of both *Salmo* species. One of us (D.E.C.) has personally observed such a fish. Alternatively, a high incidence of mortality and/or migratory disorientation may occur among hybrids following their first year of life. The

TABLE 5. Observed number of age 0+ fish from site 3 of Big Mission Creek and sites 1 and 2 of Harvey Creek expressing each genotype at the diagnostic loci after separation of individuals according to hybrid index scores. Individuals were provisionally classified as either steelhead trout (SH), cutthroat trout (CT), or as "hybrids" (HB) if their hybrid index scores were greater than 0.8, less than 0.3, or between the two values, respectively. Only allele frequencies are given for *IDH-3,4*. *G*-statistics measure goodness of fit to Hardy–Weinberg proportions. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

| | Big Mission Creek, site 3 | | Harvey Creek, sites 1 and 2 | | |
|---|---|---|---|---|---|
| Genotype | CT | HB | CT | HB | SH |
| *GLD-1* | | | | | |
| *100/100* | — | 3 | — | 2 | 7 |
| *100/110* | 23 | 53 | 12 | 30 | 3 |
| *110/110* | 8 | 2 | 60 | — | — |
| *100/120* | — | 9 | — | 3 | — |
| *110/120* | 1 | — | 8 | — | — |
| *120/120* | — | — | 1 | — | — |
| *G*-statistic | 15.42** | 58.70*** | 3.64 | 35.73*** | 0.53 |
| *ME-4* | | | | | |
| *100/100* | — | 29 | — | 10 | 10 |
| *100/110* | 15 | 35 | 3 | 18 | — |
| *110/110* | 12 | 1 | 78 | 5 | — |
| *G*-statistic | 5.92* | 8.27** | 0.06 | 0.45 | — |
| *SDH-1* | | | | | |
| *100/100* | — | 13 | 1 | 5 | 10 |
| *100/190* | — | 26 | 1 | 20 | — |
| *190/190* | 30 | 19 | 79 | 10 | — |
| *G*-statistic | — | 0.51 | 6.96[a] | 0.98 | — |
| *IDH-3,4* | | | | | |
| *100* | 0.185 | 0.594 | 0.179 | 0.700 | 0.800 |
| *72* | 0.815 | 0.406 | 0.726 | 0.183 | 0.050 |
| *44* | — | — | 0.095 | 0.117 | 0.150 |
| *N* | 31 | 56 | 74 | 30 | 10 |

[a]The *G*-statistic value for this comparison is inflated because the expected value of a genotype is less than 1.0.

absence of hybrids older than 1 yr of age, except for one questionable fish, is noteworthy with regards to a possible competitive disadvantage of hybrids compared with *clarki* or *gairdneri* juveniles, especially in freshwater during the critical overwintering period. In addition, steelhead trout and sea-run cutthroat trout exhibit distinct differences in life histories and patterns of saltwater migration (see Scott and Crossman 1973; Wydoski and Whitney 1979), and these migration patterns could conceivably become disrupted in hybrids such that hybrids fail to return to freshwater in appreciable numbers following their outmigration to saltwater. Such disorientation may occur among fish from the Beaver Creek population (*CTBC*), which are notorious for failing to return to freshwater in significant numbers following their release as smolts (Crawford 1979).

The existence of natural hybrids between *S. gairdneri* and *S. clarki clarki* also raises questions regarding the role of hatchery-origin fish. Hatchery-propagated steelhead trout and domesticated strains of resident rainbow trout have been widely planted in the Puget Sound area for decades. Nevertheless, hybridization does not appear to be widespread and species integrities are apparently being maintained. This maintenance of species integrities contrasts with the situation for the interior subspecies of cutthroat trout where introductions of non-native rainbow trout have often resulted in extensive hybridization. Whether natural hybridization between *S. gairdneri* and *S. clarki clarki* historically occurred prior to the propagation and release of hatchery fish is unknown. However, coastal cutthroat trout without basibranchial teeth (a diagnostic trait of *S.clarki*) have been found in samples from Washington and Oregon where stocking of hatchery fish has been extensive. Coastal cutthroat trout from remote areas of Alaska and British Columbia have all had basibranchial teeth (R. J. Behnke, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80521, USA, pers. comm.). Behnke attributes the lack of basibranchial teeth in coastal cutthroat trout to a hybrid influence from rainbow trout. This hypothesis remains untested, however.

We believe the prudent and far-sighted management of steelhead trout and coastal cutthroat trout along the west coast of North America requires that the mechanisms maintaining species integrities be thoroughly understood. Natural hybridization between *S. gairdneri* and *S. clarki clarki* has generally been assumed to be a rare and isolated event (Miller 1950; Needham and Gard 1959; Behnke 1972). Our findings suggest that the production of hybrid offspring may not be uncommon in streams where both species spawn. The existence of juvenile hybrids coupled with the apparent infrequency of adult hybrids further suggests that a postzygotic isolating mechanism may be contributing to the preservation of species integrities. The

TABLE 6. Estimates of gametic disequilibrium among the diagnostic loci for each of the species groups listed in Table 5. Loci 1, 2, and 3 refer to *GLD-1*, *ME-4*, and *SDH-1*, respectively. $D$, $D'$, $R$, and $\chi^2$ are as described in Table 4. $**P < 0.01$.

| Species group | Loci | $D \pm$ SE | $D'$ | $R$ | $\chi^2$ |
|---|---|---|---|---|---|
| Big Mission Creek (site 3) | | | | | |
| CT ($0.0 < I_H < 0.3$) | (1,2) | 0.053±0.021 | 0.324 | 0.533 | 7.67** |
| HB ($0.3 < I_H < 0.8$) | (1,2) | −0.011±0.009 | 0.078 | −0.151 | 1.49 |
| | (1,3) | 0.001±0.014 | 0.004 | 0.008 | 0.01 |
| | (2,3) | −0.037±0.027 | 0.315 | −0.184 | 1.94 |
| Harvey Creek (sites 1 and 2) | | | | | |
| CT ($0.0 < I_H < 0.3$) | (1,2) | 0.004±0.006 | 0.204 | 0.102 | 0.85 |
| | (1,3) | −0.003±0.003 | 0.164 | −0.063 | 0.32 |
| | (2,3) | −0.001±0.002 | 0.039 | −0.030 | 0.07 |
| HB ($0.3 < I_H < 0.8$) | (1,2) | 0.011±0.014 | 0.049 | 0.135 | 0.60 |
| | (1,3) | 0.019±0.013 | 0.094 | 0.248 | 2.15 |
| | (2,3) | −0.055±0.036 | 0.287 | −0.263 | 2.29 |

assumption of complete interfertility of *S. gairdneri* and *S. clarki clarki* (Needham and Gard 1959; Behnke 1972) has never been documented in the literature nor adequately determined experimentally by testing the fertility of F1 hybrids or backcross progeny relative to the pure parental species. The migratory fate of F1 hybrids and the contribution of hatchery fish to natural hybridization are also unknown. Extensive genetic and ecological studies are required to fully understand the biological interactions between *S. gairdneri* and *S. clarki clarki* in coastal streams of western North America.

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## References

ALLENDORF, F. W. 1975. Genetic variability in a species possessing extensive gene duplication: genetic interpretation of duplicate loci and examination of genetic variation in populations of rainbow trout. Ph.D. thesis, University of Washington, Seattle, WA. 98 p.

ALLENDORF, F. W., N. MITCHELL, N. RYMAN, AND G. STAHL. 1977. Isozyme loci in brown trout (*Salmo trutta* L.): detection and interpretation from population data. Hereditas 86: 179–190.

ALLENDORF, F. W., AND S. R. PHELPS. 1981. Isozymes and the preservation of genetic variation in salmonid fishes, p. 37–52. *In* N. Rymen [ed.] Fish gene pools. Ecol. Bull. No. 34, Stockholm.

ALLENDORF, F. W., AND F. M. UTTER. 1979. Population genetics, p. 407–454. *In* W. S. Hoar, D. J. Randall, and J. R. Brett [ed.] Fish physiology. Vol. 8. Academic Press, New York, NY.

ALLENDORF, F. W., F. M. UTTER, AND B. MAY. 1975. Gene duplication within the family Salmonidae. II. Detection and determination of the genetic control of duplicate loci through inheritance studies and the examination of populations, p. 415–432. *In* C. L. Markert [ed.] Isozymes IV: genetics and evolution. Academic Press, New York, NY.

BEHNKE, R. J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Board Can. 29: 639–671.

1979. Monograph of the native trouts of the genus *Salmo* of western North America. Published jointly by U.S. Forest Service, U.S. Fish and Wildlife Service, and U.S. Bureau of Land Management. Available from Regional Forester, 11177 W. 8th Ave., P.O. Box 25127, Lakewood, CO 80225, USA. 163 p.

BEHNKE, R. J., AND M. ZARN. 1976. Biology and management of threatened and endangered western trouts. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-28. Rocky Mountain Forestry and Range Experimental Station, Fort Collins, CO. 45 p.

BELAND, K. F., F. L. ROBERTS, AND R. L. SAUNDERS. 1981. Evidence of *Salmo salar* × *Salmo trutta* hybridization in a North American river. Can. J. Fish. Aquat. Sci. 38: 552–554.

BUSACK, C. A., AND G. A. E. GALL. 1981. Introgressive hybridization in populations of Paiute cutthroat trout (*Salmo clarki seleniris*). Can. J. Fish. Aquat. Sci. 38: 939–951.

CAMPTON, D. E. 1981. Genetic structure of sea-run cutthroat trout (*Salmo clarki clarki*) populations in the Puget Sound area. M.S. thesis, University of Washington, Seattle, WA. 180 p.

CLAYTON, J. W., AND D. N. TRETIAK. 1972. Amine–citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29: 1169–1172.

CRAWFORD, B. A. 1979. The origin and history of the trout brood stocks of the Washington Department of Game. Fishery Research Report, Washington State Game Department, Olympia, WA. 76 p.

CRAWFORD, D. R. 1925. Field characters identifying young salmonid fishes in fresh waters of Washington. Univ. Wash. Publ. Fish. 1: 64–76.

DANGEL, J. R., P. T. MACY, AND F. C. WITHLER. 1973. Annotated bibliography of interspecific hybridization of fishes of the subfamily Salmoninae. NOAA Tech. Memo. NMFS NWFC-1. U.S. Department of Commerce, Washington, DC. 48 p.

DANZMANN, R. G., AND N. E. DOWN. 1982. Isozyme expression in F1 hybrids between carp and goldfish. Biochem. Genet. 20: 1–15.

DEWITT, J. W. JR. 1954. A survey of the coastal cutthroat trout, *Salmo clarki clarki* Richardson, in California. Calif. Fish Game 40: 329–335.

DYMOND, J. R. 1928. The trout of British Columbia. Trans. Am. Fish. Soc. 58: 71–77.

ENGEL, W., P. KUHL, AND J. SCHMIDTKE. 1977. Expression of the paternally derived phosphoglucose isomerase genes during hybrid trout development. Comp. Biochem. Physiol. 56B: 103–108.

GOLD, J. R., J. C. AVISE, AND G. A. E. GALL. 1977. Chromosome cytology in the cutthroat trout series *Salmo clarki* (Salmonidae). Cytologia 42: 377–382.

HARRIS, H., AND D. A. HOPKINSON. 1976. Handbook of enzyme electrophoresis in human genetics. American Elsevier Publishing Co., New York, NY.

HARTMAN, G. F., AND C. A. GILL. 1968. Distributions of juvenile steelhead and cutthroat trout (*Salmo gairdneri* and *S. clarki clarki*) within streams in southwestern British Columbia. J. Fish. Res. Board Can. 25: 33–48.

HITZEROTH, H., J. KLOSE, S. OHNO, AND U. WOLF. 1968. Asynchronous activation of parental alleles at the tissue-specific gene loci observed on hybrid trout during early development. Biochem. Genet. 1: 287–300.

HUBBS, C. L. 1955. Hybridization between fish species in nature. Syst. Zool. 4: 1–20.

JOHNSTON, J. M., AND S. P. MERCER. 1976. Sea-run cutthroat in saltwater pens: broodstock development and extended juvenile rearing (with a life history compendium). Fishery Research Report, Project AFS-57-1, Washington State Game Department, Olympia, WA. 92 p.

LEARY, R. F., F. W. ALLENDORF, AND K. L. KNUDSEN. 1983. Consistently high meristic counts in natural hybrids between brook trout and bull trout. Syst. Zool. 32: 369–376.

LILEY, N. R. 1982. Chemical communication in fish. Can. J. Fish Aquat. Sci. 39: 22–35

LOUDENSLAGER, E. J., AND G. H. THORGAARD. 1979. Karyotypic and evolutionary relationships of the Yellowstone (*Salmo clarki bouvieri*) and west-slope (*S. c. lewisi*) cutthroat trout. J. Fish. Res. Board Can. 36: 630–635.

MARKERT, C. L., AND I. FAULHABER. 1965. Lactate dehydrogenase isozyme patterns of fish. J. Exp. Zool. 159: 319–332.

MAY, B., J. E. WRIGHT, AND M. STONEKING. 1979. Joint segregation of biochemical loci in Salmonidae: results from experiments with *Salvelinus* and review of the literature on other species. J. Fish. Res. Board Can. 36: 1114–1128.

MCCONNELL, R. J., AND G. R. SNYDER. 1972. Key to field identification of anadromous juvenile salmonids in the Pacific Northwest. NOAA Tech. Rep., NMFS Circ. No. 366, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, Seattle, WA. 6 p.

MILLER, R. R. 1950. Notes on the cutthroat and rainbow trouts with the description of a new species from the Gila River, New Mexico. Occas. Pap. Mus. Zool., Univ. Mich., No. 529. University of Michigan Press, Ann Arbor, MI. 42 p.

NEEDHAM, P. R., AND R. GARD. 1959. Rainbow trout in Mexico and California with notes on the cutthroat series. Univ. Calif. Publ. Zool. 67: 1–124.

NEFF, N. A., AND G. R. SMITH. 1979. Multivariate analysis of hybrid fishes. Syst. Zool. 28: 176–196.

NYMAN, L. 1970. Electrophoretic analysis of hybrids between salmon (*Salmo salar*) and trout (*Salmo trutta*). Trans. Am. Fish. Soc. 99: 229–236.

OHNO, S. 1969. The preferential activation of maternally derived alleles in development of interspecific hybrids. Wistar Symp. Monogr. 9: 137–150.

PAYNE, R. H., A. R. CHILD, AND A. FORREST. 1972. The existence of natural hybrids between the European trout and the Atlantic salmon. J. Fish Biol. 4: 233–236.

PHILLIPS, C., W. FREYMOND, D. CAMPTON, AND R. COOPER. 1980. Skagit River salmonid studies, 1977–1979. Fishery Research Report 80-24, Washington State Game Department, Olympia, WA. 132 p.

REINITZ, G. L. 1977. Electrophoretic distinction of rainbow trout (*Salmo gairdneri*), west-slope cutthroat trout (*S. clarki*), and their hybrids. J. Fish. Res. Board Can. 34: 1236–1239.

RIDGWAY, G. J., S. W. SHERBURNE, AND R. D. LEWIS. 1970. Polymorphism in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99: 147–151.

ROSS, M. R., AND T. M. CAVENDER. 1981. Morphological analyses of four experimental intergeneric cyprinid hybrid crosses. Copeia 1981: 377–387.
SCHRECK, C. B., AND R. J. BEHNKE. 1971. Trouts of the upper Kern River Basin, California, with reference to systematics and evolution of western North American *Salmo*. J. Fish. Res. Board Can. 28: 987–998.
SCHWARTZ, F. J. 1972. World literature to fish hybrids with an analysis by family, species, and hybrid. Publ. Gulf Coast Res. Lab. Mus. No. 3: 328 p.
SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.
SHAW, C. R., AND R. PRASAD. 1970. Starch gel electrophoresis of enzymes — a compilation of recipes. Biochem. Genet. 4: 297–320.
SIMON, R. C., AND R. E. NOBLE. 1968. Hybridization in *Oncorhynchus* (Salmonidae). I. Viability and inheritance in artificial crosses of chum and pink salmon. Trans. Am. Fish. Soc. 97: 109–118.
SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, CA. 776 p.
SOLOMON, D. J., AND A. R. CHILD. 1978. Identification of juvenile natural hybrids between Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.). J. Fish Biol. 12: 499–501.
THORGAARD, G. H. 1983. Chromosomal differences among rainbow trout populations. Copeia 1983: 650–662.
UTTER, F. M., F. W. ALLENDORF, AND B. MAY. 1979. Genetic basis of creatine kinase isozymes in skeletal muscle of salmonid fishes. Biochem. Genet. 17: 1079–1091.
UTTER, F. M., D. CAMPTON, S. GRANT, G. MILNER, J. SEEB, AND L. WISHARD. 1980. Population structures of indigenous salmonid species of the Pacific Northwest, p. 285–304. *In* W. J. McNeil and D. C. Himsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press and Oregon State University Sea Grant College Program, Corvallis, OR.
UTTER, F. M., H. O. HODGINS, AND F. W. ALLENDORF. 1974. Biochemical genetic studies of fishes: potentialities and limitations, p. 213–238. *In* D. C. Malins and J. R. Sargent [ed.] Biochemical and biophysical perspectives in marine biology, Vol. 1. Academic Press, New York, NY.
WEIR, B. S. 1979. Inferences about linkage disequilibrium. Biometrics 35: 235–254.
WYDOSKI, R. S., AND R. R. WHITNEY. 1979. Inland fishes of Washington. University of Washington Press, Seattle, WA, and London. 220 p.

## Appendix

We define the hybrid index ($I_H$) between species $X$ and $Y$ for an individual as

$$I_H = 1.0 - \left[\frac{\log_{10}(p_x)}{\log_{10}(p_x) + \log_{10}(p_y)}\right]$$

where

$$p_x = \prod_{i=1}^{L} k_i \prod_{j=1}^{A_i} (X_{ij})^{m_{ij}}$$

$$p_y = \prod_{i=1}^{L} k_i \prod_{j=1}^{A_i} (Y_{ij})^{m_{ij}}$$

and

$X_{ij}$ = the average frequency of the $j$th allele at the $i$th locus for species $X$

$Y_{ij}$ = the average frequency of the $j$th allele at the $i$th locus for species $Y$

$m_{ij}$ = the number of alleles of the $j$th type expressed at the $i$th locus by the individual being evaluated ($m_{ij}$ = 0, 1, or 2 for disomic loci; $m_{ij}$ = 0, 1, 2, 3, or 4 for tetrasomic or duplicated loci)

$A_i$ = the total number of known alleles at the $i$th locus for the two species combined

$k_i$ = the binomial sampling coefficient associated with the genotype of the individual at the $i$th locus ($k_i$ = 1 or 2 for disomic loci; $k_i$ = 1, 4, 6, 12, or 24 for tetrasomic loci with four or more distinct alleles)

$L$ = the number of diagnostic loci used to distinguish the two species

The index is calculated for each individual. The estimated average frequencies ($X_{ij}$'s and $Y_{ij}$'s) of all known alleles at loci diagnostic for distinguishing the two parental species are used as input parameters for the index function. The reader should note that $p_x$ and $p_y$ are the conditional probabilities that an individual's combined genotype at all diagnostic loci could have arisen by random mating within species $X$ and $Y$, respectively, given the average allele frequencies for the two species and assuming linkage equilibrium among loci. These probabilities will generally range from $10^{-1}$ to $10^{-15}$ depending on the number of distinguishing loci and the average frequences of the alleles. Logarithms (base 10) of the $p_x$'s and $p_y$'s are therefore used in order to compare the magnitude of the probabilities rather than the probabilities themselves. A change of 0.1 in the value of the index therefore corresponds to a factor of ten (10×) regarding the relative probability that an individual belongs to species $X$ or $Y$. The index can assume any value between 0.0 and 1.0. We subtract the quotient (quantity in brackets) from one (1.0) so that individuals from species $X$, the species in the numerator, will be associated with values of the index near one (1.0). In this paper, species $X$ is *S. gairdneri* and species $Y$ is *S. clarki clarki*. Values of the index close to 1.0 therefore indicate that the individual's genotype has a high probability of having been produced within *S. gairdneri* relative to being produced within *S. clarki clarki* and vice versa for index values close to 0.0.

Average allele frequencies for each of the two species were taken from Table 1. We have, however, substituted a frequency of 0.001 for alleles in Table 1 with a frequency of zero ($X_{ij} = 0$ or $Y_{ij} = 0$). Genotypes at *IDH-3,4* were interpreted in terms of two disomic loci, and individuals with genotypes of the form AABB were treated as being homozygous, not heterozygous, at both loci. The values of $k_i$ at *IDH-3,4* were therefore 1, 2, or 4 depending on whether an individual expressed a genotype of the form AABB, AAAB, or ABCD, respectively. These values of $k_i$ at *IDH-3,4* therefore resulted in a conservative contribution of this duplicated locus to the overall value of the index for each individual.

### Numerical Example

Suppose an individual fish expressed the following composite genotype at the diagnostic loci: *GLD-1(100/110)*; *IDH-3,4-(100/72/72/44)*; *ME-4(110/110)*; *SDH-1(100/190)*. Then using the average allele frequencies given for the two species in Table 1:

$$p_x = [2(0.949)(0.020)][2(0.731)(0.084)^2(0.154)] \times [(0.017)^2][2(1.000)(0.001)] = 3.49 \times 10^{-11}$$

$$p_y = [2(0.090)(0.894)][2(0.115)(0.796)^2(0.078)] \times [(0.972)^2][2(0.100)(0.899)] = 3.11 \times 10^{-4}$$

The value of the hybrid index for this fish is therefore

$$I_H = 1.0 - \left[\frac{\log_{10}(3.49 \times 10^{-11})}{\log_{10}(3.49 \times 10^{-11}) + \log_{10}(3.11 \times 10^{-4})}\right] = 0.251.$$

The value of this index is less than 0.30 and we would therefore have classified this individual as a cutthroat trout according to the criteria described in the text (see Fig. 2 and 3).

# Feeding Ecology of the Sauger (*Stizostedion canadense*) in a Large River

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Wahl, D. H., and L. A. Nielsen. 1985. Feeding ecology of the sauger (*Stizostedion canadense*) in a large river. Can. J. Fish. Aquat. Sci. 42: 120–128.

In stomachs of 550 sauger (*Stizostedion canadense*) collected by gillnetting in the Ohio River during June 1980 through August 1981, *Dorosoma cepedianum* were the most abundant prey (42% of all identified prey), followed by *Notropis atherinoides* (28%), *Aplodinotus grunniens* (16%), and *Ictalurus punctatus* (12%). Annual food consumption of sauger averaged 1.1% of the body weight per day. Growth and daily ration followed similar patterns, being high from September to January (maximum in October) and low from March to August. Rapid growth and high food consumption throughout fall and early winter were related to an extended period of high temperatures and increased availability of *Dorosoma cepedianum*. The annual period of growth and food consumption was longer and peaked later in the year in the river than those previously observed in other types of aquatic systems.

Les estomacs de 550 dorés noirs (*Stizostedion canadense*) capturés au filet maillant dans la rivière Ohio, de juin 1980 à août 1981, contenaient, par ordre d'importance, les proies suivantes : *Dorosoma cepedianum* (42 % de toutes les proies identifiées), *Notropis atherinoides* (28 %), *Aplodinotus grunniens* (16 %) et *Ictalurus punctatus* (12 %). La consommation alimentaire annuelle des dorés noirs correspondait en moyenne à 1,1 % du poids corporel par jour. La croissance et la quantité d'aliments ingérés chaque jour présentaient des allures semblables : elles étaient élevées de septembre à janvier (maximum en octobre) et faibles de mars à août. Il y avait corrélation, d'une part, entre la croissance rapide et la forte consommation alimentaire tout au long de l'automne et au début de l'hiver et, d'autre part, une période de températures élevées et de plus grande disponibilité de *Dorosoma cepedianum*. La saison de croissance et d'alimentation était plus longue et atteignait son maximum plus tard au cours de l'année dans cette rivière, comparativement à celle notée antérieurement dans d'autres types de systèmes aquatiques.

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Aquatic predator–prey relationships have been evaluated primarily in lakes, impoundments, and small streams, rather than in large rivers (Campbell 1979). Rivers have been ignored because sampling is difficult (Mann 1975) and because the large size, high volume of flow, and multiple uses of rivers make manipulation of the riverine habitat as experimental treatments almost impossible (Campbell 1979). This absence of information on rivers is particularly critical for percids, as predator–prey interactions among these fishes probably depend as much on the ecosystem as on the species (Regier et al. 1969; MacLean and Magnuson 1977; Nielsen 1980). Predator–prey relationships involving *Stizostedion* spp. have been studied extensively in lakes and reservoirs (Parsons 1971; Forney 1974, 1977a; McGee et al. 1977; Nielsen 1980; Minton and McLean 1982). For these systems, a generalized description of annual predation and growth would include a bimodal pattern with a primary peak in food consumption and growth in early summer, a slump in midsummer, and a secondary peak in the fall. Food consumption and growth then decline rapidly in late fall, with minimal growth and consumption over winter. Similar attempts have not been made to evaluate patterns of annual predation and growth in large rivers. Previous studies in large rivers have been restricted to evaluations of fish growth (Mann 1976), food habits (Griffiths 1976; Mann 1976), and production (Williams 1965; Backiel 1971; Mathews 1971).

Several environmental factors in large rivers may cause different predation patterns in rivers than in lakes or reservoirs. In particular, patterns of growth and food consumption in large rivers like the Ohio may differ from those in other aquatic systems. Annual temperature patterns, flow, and turbidity levels all differ between lentic and lotic systems (Oglesby et al. 1972; Hynes 1973; Whitton 1975). Continual flow of water and greater vertical mixing in rivers cause water temperatures in lotic systems to be lower during summer and higher during winter than those observed in lentic systems. Water temperatures affect fish metabolism and behavior (Aggus 1979), and as a result influence patterns of growth and food consumption (Hokanson 1977; Kitchell et al. 1977a, 1977b). Because increasing flow rates means higher fish metabolism, food consumption and growth may be affected (Allen 1969; Aggus 1979). Turbidity can also operate to reduce food consumption, as Gardner (1981) has found for bluegills (*Lepomis macrochirus*) in laboratory experiments. Limited research on large European rivers has verified the differences in predation patterns between lakes and large rivers suggested by the environmental

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differences. Popova and Sytina (1977) found that daily ration of pikeperch (*Stizostedion lucioperca*) and perch (*Perca fluviatilis*) stayed higher longer and peaked earlier in the Volga River than in either Pskov-Chudskof Lake or Rybinsk Reservoir. Griffiths (1976) observed that perch in the Selvyn River, New Zealand, continued feeding through midwinter. Seasonal patterns of food consumption have not been fully elaborated in large rivers, nor have they been adequately linked to patterns of growth and existing environmental conditions.

The lack of data from large river systems like the Ohio represents a substantial gap in our understanding of predator–prey interactions. This study was designed to fill the void by describing the predator–prey relationships of a dominant carnivore for an annual cycle in the Ohio River. Comparison with patterns of predation in other systems will provide a better understanding of the functioning of predator–prey relationships in large river ecosystems.

## Materials and Methods

### Study Area

We sampled the Gallipolis Pool of the Ohio River, from the Racine Lock and Dam (River Mile 237) downstream to the junction of the Kanawha River (River Mile 266). Because the U.S. Army Corps of Engineers manages the Ohio River for navigation, the river has relatively steep banks, uniform depth, and a scarcity of aquatic macrophytes. The river flows in a narrow valley for most of its length with few backwaters. The large drainage area of 528 127 $km^2$ causes high flow rates when snowmelt or rainfall is high (Preston and White 1978). Monthly flow rates and transparency varied during the study, with periods of high flow corresponding to times of high turbidity (Table 1). The annual temperature cycle reached the maximum during July and the minimums in January and February. The Ohio River fish fauna includes over 150 species and has been described extensively (Trautman 1981).

### Data Collection

Sauger (*Stizostedion canadense*) were collected by gill net at six locations during June 1980 through August 1981. Each monofilament gill net was 38 m long, 1.8 m deep, and contained five equal panels with 3.8-, 5.1-, 6.4-, 7.6-, and 10.2-cm stretched mesh. Samples were collected over 2–7 d near the middle of each month. Nets were lifted and emptied every 3–4 h over a 24-h period from May to October, twice a day in November and April, and once a day in January and March. Lift intervals were kept short relative to estimated rates of gastric evacuation to minimize the digestion of stomach contents between fish capture and emptying of nets (Eggers 1977). Scale samples, total length (to 0.5 cm), and weight (to 1.0 g) were taken from each sauger.

After removal from gill nets, the body cavity of the fish was injected with 10% buffered formalin and placed on ice to reduce further digestion. Regurgitation of food was rarely observed (<2.0%) during capture of fish in any month, and fish with signs of regurgitated food were eliminated from further analyses. In the laboratory, stomach contents were removed, and each prey item was measured in length (to 1.0 mm) and weighed (to 0.1 g). Ingested prey were measured as total, standard, or backbone length depending on stage of digestion. Prey items were identified to species; partially digested fish were identified through structures resistant to digestion. The few fish that could not be identified were eliminated from further analyses (most had reached advanced stages of digestion). Weight of each identified prey item at time of ingestion was then predicted using length–weight relationships developed for the major prey species (Wahl 1982). Prey samples used in formulating these equations were collected by seining during each month at locations and dates corresponding to gillnet sets. Total length (to 1.0 mm), standard length (to 1.0 mm), and weight (to 0.1 g) were recorded for each fish used in the regression equations. The vertebral column was then extracted from each fish for use in the determination of backbone length (to 1.0 mm) (Minton and McLean 1982).

TABLE 1. Average values for physical parameters of the Ohio River on sample dates during June 1980 through August 1981.

| | Sampling period | Water temperature (°C)[a] | Flow ($cm \cdot s^{-1}$)[b] | Secchi disc (m)[b] |
|---|---|---|---|---|
| 1980 | June | 22.6 | 21.0 | 0.71 |
| | July | 27.4 | 21.9 | 0.78 |
| | August | 25.8 | 100.5 | — |
| | September | 25.1 | 23.5 | 0.84 |
| | October | 19.7 | 26.7 | 0.75 |
| | November | 9.6 | 29.6 | 0.51 |
| 1981 | January | 2.9 | 36.4 | 0.55 |
| | March | 6.4 | 63.5 | 0.63 |
| | April | 13.5 | 54.0 | 0.20 |
| | May | 14.3 | 98.2 | 0.20 |
| | June | 23.5 | 83.1 | 0.28 |
| | July | 26.7 | 22.5 | 0.69 |
| | August | 26.6 | 43.3 | 0.78 |

[a]Data from Ohio River Valley Sanitation Commission, Cincinnati, OH (unpubl. data), collected hourly at Addison, OH (River Mile 260.0).

[b]Data collected daily at Cheshire, OH (River Mile 257.7).

### Digestion Rates

Digestion rates for saugers were calculated using the linear relationships between the percentage of food evacuated from the stomach and time as determined by Swensen and Smith (1973). These equations were presumed applicable to Ohio River sauger, as Swenson and Smith (1973) found no significant differences in digestion rates between walleye (*Stizostedion vitreum vitreum*) and sauger or among individuals taken from three different lakes. The linear form is consistent with other laboratory studies (Hofmann 1969) and is compatible with results from field evaluations (Forney 1977a).

Swenson and Smith (1973) evaluated digestion rates over a narrower range of temperatures (14.5–20°C) than those encountered in this study. Therefore, data from Hofmann (1969) were used to calculate the digestion rates for walleye at temperature as

$$\ln Y = -1.1899 \ln X + 6.5443, \quad r^2 = 0.96$$

where $Y$ = time for 100% digestion and $X$ = temperature (degrees Celsius). The slope of the relationship was then used to adjust the regression equations of Swenson and Smith (1973) to temperatures outside the range they studied. These temperature adjustments gave equations describing relations between percentage digestion ($Y$), time ($X$, hours), meal size ($X_1$, milligrams per gram), and temperature ($T$) for three prey size ranges

as follows:

$<1.1$ g: $Y = 42.375 + 5.620e^{1.899(\ln T - \ln 20.0)}(X) - 0.493(X_1)$

1.1–2.5 g: $Y = 21.469 + 4.797e^{1.1899(\ln T - \ln 14.5)}(X) - 0.149(X_1)$

$>2.5$ g: $Y = 0.279 + 4.321e^{1.1899(\ln T - \ln 14.5)}(X) - 0.205(X_1)$.

The exponential nature of these relationships is consistent with those developed for other fishes (Molnar et al. 1966; Steigenberger and Larkin 1974; Windell et al. 1976).

### Daily Ration and Growth Rates

Estimates of daily ration by sauger were made using Swenson and Smith's (1973) equation. This method was chosen over other available methods of estimating food consumption (Popova and Sytina 1977; Elliott and Persson 1978; Nakashima and Leggett 1978; Diana 1979) because it incorporates information on fish size, food size, and meal size and does not assume continual feeding throughout the day. The daily ration ($C_d$, milligrams per gram per day) of sauger was calculated by estimating the ration ($C_{t,s}$) during a short time interval ($t$; 2 h in this study) for each of the three prey size ranges (s) for which digestion rate equations were developed and then summing them across time intervals and prey ranges as

$$C_d = \sum_{t=1}^{12} \sum_{s=1}^{3} C_{t,s}.$$

The ration for each 2-h interval and prey range was estimated in three steps. First, weight of each prey item at the time of consumption was estimated from length–weight relations described earlier. Weight of a feeding was then expressed in terms of body weight of the sauger that consumed it. Second, the time since ingestion for each prey fish observed in a sauger stomach was determined from the relative state of digestion, total meal size, and temperature using the appropriate digestion rate equation described earlier; the time interval during which that prey item was consumed was determined by subtracting time since ingestion from time of capture. Third, the number of sauger that could have been observed to contain a prey item of that size during a particular time interval was computed by subtracting time to 90% digestion from time of capture for each sauger (that is, a sauger was considered part of the sample for all time intervals from time of capture back to the limits of time when ingested food would have been undetectable). Two-hour ration ($C_{t,s}$, milligrams per gram per 2 h), in mathematical terms, was calculated as

$$C_{t,s} = SC/F$$

where $SC$ = total weight of prey of size $s$ consumed during interval $t$ and $F$ = total number of sauger that could have, at time of capture, held prey of size $s$ consumed during interval $t$.

To evaluate the relationship between daily ration and growth, monthly instantaneous growth rates were calculated between each pair of samples for each sauger age class as

$$G = \frac{\ln w_{t_2} - \ln w_{t_1}}{\Delta t} \times 100$$

where $w_{t_1}$ = median wet weight of any given sample, $w_{t_2}$ = median wet weight of the subsequent sample, and $\Delta t$ = number of days between samples. A composite monthly $G$ for the population was calculated by averaging values of $G$ for the four abundant year classes, weighted according to relative abundance in monthly samples. Absolute growth was also estimated for intervals between samples and expressed in relative (grams per gram) terms based on average sauger weight for the interval. Food consumption (grams per gram) was determined for the same periods using an average daily ration based on estimates at the beginning and end of the interval. Division of growth (grams per gram) by food consumption (grams per gram) gave an estimate of food conversion efficiency.

## Results

### Food Habits of Sauger

Enumeration of stomach contents of 550 sauger collected from the Ohio River during June 1980 through August 1981 revealed that gizzard shad (*Dorosoma cepedianum*) and emerald shiners (*Notropis atherinoides*) were the most common prey throughout the year, followed by freshwater drum (*Aplodinotus grunniens*), channel catfish (*Ictalurus punctatus*), and mimic shiners (*Notropis volucellus*) (Table 2). Other identified prey as a group made up less than 1% of the total fish prey observed. Invertebrates were infrequent, occurring in only 6.4% of all sauger examined. Empty stomachs were common, occurring in 10–73% of the fish sampled during each month.

The relative occurrence of the various prey items in sauger stomachs varied by month. Gizzard shad made up over half of the prey items in both number (Table 2) and weight (Fig. 1) during September through January. Emerald shiners were numerically important during most of the year, declining somewhat from October through January. Emerald shiners were more important in terms of number than in weight. Freshwater drum and channel catfish became substantial portions of the diet in July and August; the exact timing of occurrence in the stomachs varied slightly between the two years sampled. Mimic shiners were uncommon in stomachs in all samples. Other fish species were seldom eaten during most of the year, but were most common in stomachs in March and April. Invertebrates were most common in stomachs during spring (Fig. 1).

### Ration and Growth

Times for representative prey items to reach 90% digestion varied from a low of 6 h in July to a high of 7.8 d in January (Table 3). Water temperatures were highest, and sauger fed on relatively smaller sized prey in July as compared with the low water temperatures and larger prey consumed during January. The values determined for Ohio River sauger were similar to those developed for other piscivorous species of fish at comparable temperatures (Seaburg and Moyle 1964; Forney 1977a; McGee et al. 1977; Diana 1979).

Seasonal patterns of sauger growth in length and weight were similar for the 1977–79 year classes (Kruskal-Wallis; $p > 0.50$ for length, $p > 0.90$ for weight). The period of most rapid growth in weight occurred during the months from September through March, with some additional growth also observed during June to August (Fig. 2). Patterns of growth in length were similar to those observed for weight. The pattern of growth for the 1980 year class also appeared similar, but low sample sizes from December through May prevented detailed comparison with other cohorts.

Preliminary tests showed that monthly median meal sizes

TABLE 2. Number of prey items found in stomachs of sauger collected in 1980 and 1981 from the Ohio River. Numbers of sauger sampled are given in parentheses.

| Prey item | June (62) | July (55) | Aug. (70) | Sept. (47) | Oct. (54) | Nov. (70) | Jan. (42) | Mar. (54) | Apr. (44) | May (52) | Total (550) | % of total fish prey |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Dorosoma cepedianum* | 1 | 0 | 12 | 14 | 43 | 66 | 77 | 1 | 2 | 1 | 217 | 42 |
| *Notropis atherinoides* | 15 | 37 | 42 | 12 | 11 | 9 | 3 | 2 | 2 | 13 | 146 | 28 |
| *Aplodinatus grunniens* | 0 | 2 | 73 | 0 | 6 | 0 | 1 | 0 | 1 | 0 | 84 | 16 |
| *Ictalurus punctatus* | 0 | 30 | 29 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 61 | 12 |
| *Notropis volucellus* | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 5 | 1 |
| *Lepomis macrochirus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 |
| *Lamptera aepyptera* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 |
| *Morone chrysops* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Ambloplites rupestris* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| Unidentified fish | 1 | 0 | 3 | 2 | 0 | 5 | 0 | 2 | 4 | 1 | | |
| Invertebrates | | | | | | | | | | | | |
| Cl. Insecta | | | | | | | | | | | | |
| Ephemeroptera | 10 | 1 | 0 | 1 | 0 | 0 | 0 | 13 | 1 | 1 | | |
| Trichoptera | 3 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | | |
| Amphipoda | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 29 | 1 | 0 | | |
| Odonata | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Diptera | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | | |
| Cl. Crustacea | | | | | | | | | | | | |
| Decapod | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| No. of empty stomachs | 33 | 21 | 20 | 22 | 16 | 26 | 4 | 36 | 31 | 38 | | |

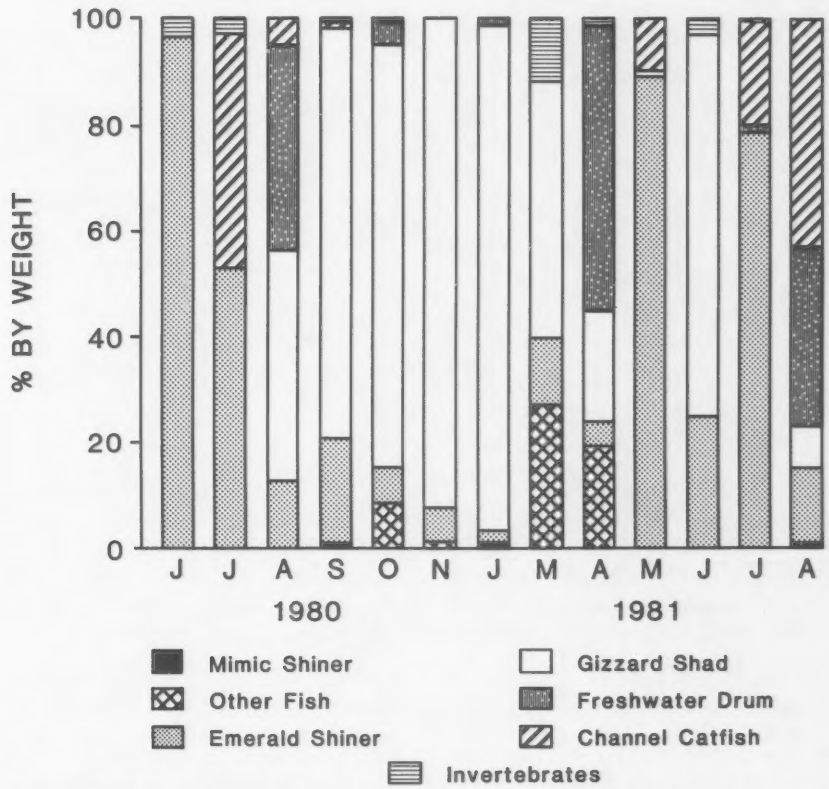


FIG. 1. Change in species composition of sauger stomach contents, based on relative weight, from saugers collected in the Ohio River, June 1980 through August 1981.

TABLE 3. Comparison of observed average daily ration for sauger in the Ohio River with estimated daily maintenance rations at corresponding temperatures.

| | Month | No. of saugers sampled | Mean water temperature (°C) | Average ingested prey weight (g) | Time to 90% digestion (h)[a] | Average daily ration ($mg \cdot g^{-1} \cdot d^{-1}$) | Maintenance ration ($mg \cdot g^{-1} \cdot d^{-1}$) |
|---|---|---|---|---|---|---|---|
| 1980 | June | 17 | 22.6 | 3.26 | 8.2 | 14.3 | 12.5 |
| | July | 12 | 27.4 | 0.23 | 6.0 | 6.9 | 17.2 |
| | August | 24 | 25.8 | 1.38 | 7.6 | 11.4 | 15.5 |
| | September | 47 | 25.1 | 3.19 | 10.0 | 19.3 | 14.8 |
| | October | 54 | 19.7 | 6.12 | 16.0 | 37.7 | 10.3 |
| | November | 70 | 9.6 | 7.77 | 39.8 | 12.9 | 5.2 |
| 1981 | January | 42 | 2.9 | 10.67 | 186.5 | 6.5 | 3.3 |
| | March | 54 | 6.4 | 1.82 | 38.5 | 0.5 | 4.2 |
| | April | 44 | 13.5 | 5.07 | 19.7 | 2.0 | 6.8 |
| | May | 52 | 14.3 | 2.09 | 16.5 | 2.1 | 7.2 |
| | June | 45 | 23.5 | 4.03 | 8.8 | 10.4 | 13.3 |
| | July | 43 | 26.7 | 0.47 | 6.1 | 5.5 | 16.4 |
| | August | 46 | 26.6 | 0.51 | 6.6 | 11.9 | 16.3 |

[a]Representative value for month using average prey sizes, meal sizes, and temperature.

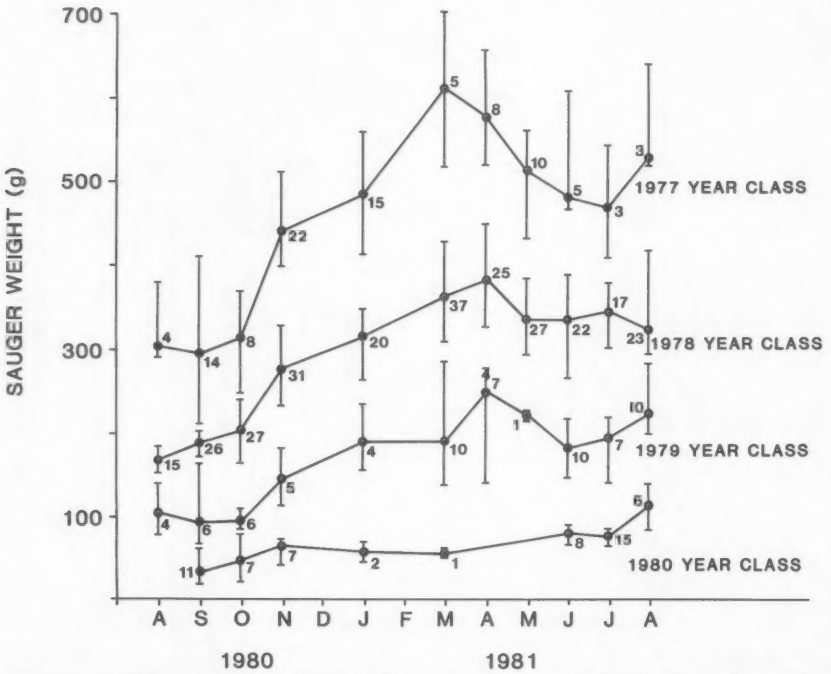


FIG. 2. Monthly median weights for 1977–80 year classes of sauger in the Ohio River. Upper and lower limits represent interquartile range. Sample sizes are listed next to each median value.

(milligrams per gram) were similar for the 1977–80 year classes of sauger (Friedman test, $p = 0.685$), and that male and female saugers consumed similar monthly meal sizes (Wilcoxon signed rank test, $p > 0.05$). Although the reduced sample sizes caused by splitting into several classes could have prevented the detection of any actual differences in these analyses, the results are consistent with an expectation that meal size relative to total weight should not vary among sex or age. Differences in daily ration between age classes of sauger should be most significant during the first year when age 0+ fish may be preying largely on invertebrates. Age 0+ sauger were not captured until after early September, and estimates of daily ration (milligrams per gram per day) of these and age 1+ and older sauger after this period were similar (Wilcoxon signed rank test, $p > 0.625$). As a result of these tests, fish from the four most abundant age classes (0+ to 3+) were pooled by month to derive estimates of the average

TABLE 4. Food conversion efficiency for the 1977–80 sauger year classes, by monthly intervals, August 1980 – January 1981, and on an annual basis, August 1980 – August 1981.

| Period | Period length (d) | No. of saugers | Consumption ($g \cdot g^{-1}$) | Growth ($g \cdot g^{-1}$) | Conversion efficiency (%) |
|---|---|---|---|---|---|
| Aug. 10 – Sept. 16 | 38 | 69 | 0.5833 | 0.0771 | 13.2 |
| Sept. 17 – Oct. 12 | 26 | 105 | 0.7410 | 0.0741 | 10.0 |
| Oct. 13 – Nov. 20 | 39 | 114 | 0.9867 | 0.3254 | 32.9 |
| Nov. 21 – Jan. 28 | 68 | 106 | 0.6596 | 0.1187 | 18.0 |
| Monthly total | | | | | |
| Aug. 10 – Jan. 28, 1980 | 171 | 234 | 2.9706 | 0.5377 | 18.1 |
| Annual total | | | | | |
| Aug. 10, 1980 – Aug. 7, 1981 | 362 | 494 | 4.0342 | 0.7947 | 19.7 |

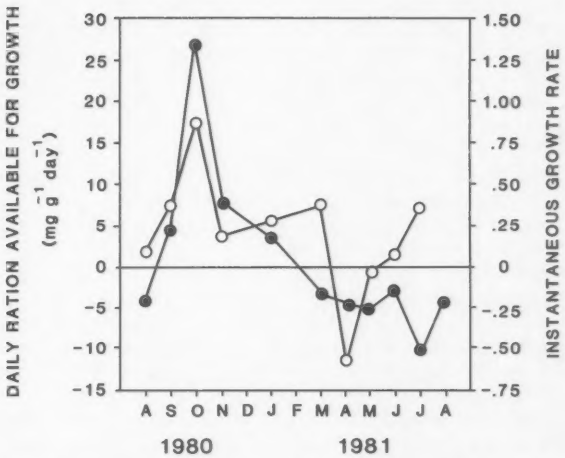


FIG. 3. Comparison of the portion of average daily ration available for growth (●) with weighted instantaneous growth rates (○) for the 1977–80 sauger year classes, August 1980 – August 1981.

daily ration (milligrams per gram per day) for the population (Table 3).

Annual food consumption for Ohio River sauger averaged 1.1% of the body weight per day. The annual pattern of daily ration followed a bimodal distribution (Table 3), with a major peak in October and a smaller peak in June. During September through January, when growth was most rapid, food consumption averaged 1.8% of the body weight per day.

Monthly patterns of daily ration and growth were compared by first calculating maintenance rations using Kelso's (1972) relations between maintenance requirements of walleye and temperature. (The original equation (Kelso 1972) relating maintenance rations ($M$ milligrams per gram per day) and temperature ($T$ degrees Celsius) was incorrect and should have been given as $M = (10^{1.286+0.029T})/7$ (J. R. M. Kelso, pers. comm.)). Subtracting calculated maintenance rations from observed rations of sauger (Table 3) gives a representative estimate of the daily energy available for growth during each month. Instantaneous growth rates ($G$), weighted by sample size for the four year classes, and the portion of daily ration available for growth (milligrams per gram per day) followed similar monthly patterns for Ohio River sauger (Spearmans rank correlation, $p < 0.05$) (Fig. 3). Ration levels were sufficient for growth from September to January, peaking in October. Ration was below maintenance at other times of the year, with corresponding instantaneous growth rates near or below zero. The major difference between the patterns occurred in summer of 1981, when growth rates increased while energy available for growth remained below maintenance levels.

### Food Conversion Efficiency

Food conversion efficiency for the 1977–80 sauger year classes, weighted by sample size, average 19.7% for the entire year (Table 4). Food conversion efficiencies varied from August through January, but averaged approximately 18.1%. Conversion efficiency peaked during October and November, corresponding to the period of maximum daily rations. Although growth was observed in two of four sauger year classes during the period from January through March, fish from these months were not included in calculations of growing season conversion efficiency due to the poor correlation during this period between growth and portion of daily ration available for growth.

## Discussion

Prey assemblages and the resulting species use by sauger in the Ohio River were similar to those occurring in a variety of aquatic systems (Priegel 1963; Swenson and Smith 1973; Rawson and Scholl 1978; Minton and McLean 1982). Growth rates of sauger were also within limits reported for this species throughout its geographic range (Carlander 1950; Hassler 1957; Nelson and Walburg 1977). Annual growth and longevity were intermediate between those taken from more northerly and southerly waters. However, the timing of growth and food consumption within the annual cycle differed in the Ohio River.

Instantaneous growth rates and daily energy available for growth followed similar annual patterns, agreeing closely over 6 of the 10 monthly intervals sampled. In only two of the remaining four intervals did these data diverge substantially. Discrepancies between growth and ration data may be the result of several factors. Whereas the catch of more than 40 sauger per sample is substantial for a piscivore in a large river, it is small in terms of computing a populations bioenergetics budget. This neccessitated the pooling of data from various subunits as deemed reasonable from the literature and our preliminary analyses. Annual growth patterns were similar for the four abundant age classes examined, so these were pooled to represent growth for the population. Diana (1983) observed

similar stable allocation of energy to growth beginning at age 1 for northern pike (*Esox lucius*). Daily ration estimates of male and female sauger did not differ significantly in this study, in contrast with the findings of Diana (1979) that female northern pike of a given age had significantly higher rations than males. Previous work with sauger, however, has not detected differences in ration estimates between sexes (Swenson and Smith 1976; Minton and McLean 1982). Although such pooling appears justified, subtle variations in sample composition across months may affect the relation between individual pairs of data.

Certain methodological constraints may also have affected the precision of estimates of instantaneous growth and available energy. Undetected regurgitation of food items prior to removal from the nets would reduce estimates of daily ration (Diana 1983); such regurgitation may be seasonal if attenuated species, like emerald shiner, which comprise more of the diet in summer, are more likely to be reguritated than compressed species, like gizzard shad, that become important dietary items in the fall. Daily ration estimates taken at monthly intervals were assumed to represent the entire month, but substantial variation among dates within a month is likely due to random and environmental factors. The use of digestion rate and maintenance ration data derived for walleye may also have affected precision of ration estimates.

Despite these restrictions, the general agreement across months between estimates of instantaneous growth and daily ration available for growth suggests that estimates were accurate over the annual cycle. Data from large rivers are critical to the development of a comprehensive model of bioenergetics. Study of large rivers lags considerably behind that of lentic systems, since sampling conditions are among the most restrictive of any inland habitat (Mann 1975; Campbell 1979). Data from this study allow quantitative evaluation of ration and growth of a piscivore in a large river and a comparison with the more extensive data from lentic environments. The pattern of ration and growth of sauger in the Ohio River varied from those previously observed for percids in lentic systems. Environmental characteristics present in the Ohio River may have influenced some aspects of predator–prey relationships. Below, we interpret sauger predation and energetics in terms of the conditions present in this system.

### Spring

Lowest growth and food consumption of sauger in the Ohio River occurred during March through May. High turbidity levels, low food availability, and a spawning fast by sauger may all have been important in determining the observed reduction in feeding. Turbidity levels were extremely high during a portion of this period (April–May) and are known to reduce feeding rates in sight-feeding fishes (Gardner 1981). Correlation between turbidity levels and feeding rates was not apparent, however, at other times of the year, suggesting that turbidity was unimportant in determining levels of food consumption throughout the year. Food availability, based on seine catches, apparently reached the lowest levels during March through June in the Ohio River and may have contributed to reduced levels of food consumption (Wahl 1982). Jenkins (1979) observed reduced biomass of available prey in southeastern reservoirs during this time. Sauger were feeding on invertebrates and miscellaneous fishes during these months, as typical of periods of reduced primary prey availability (Priegel 1963). Levels of food consumption increased in June, however, before the new year classes of primary prey species appeared in sauger stomachs and in seine catches (Wahl 1982).

This information suggests that the reduction in rations of sauger may have been due to alterations in sauger behavior during spawning. Nelson (1968) observed initiation of spawning by sauger at temperatures near 6.1°C. Water temperature exceeded 6.1°C in the Ohio River in mid-March, and the percent of spent sauger captured increased steadily from March (0%) through April (12%), May (37%), and June (100%). Diana (1979) observed a spawning fast by northern pike in Alberta under conditions analogous to those accompanying reduced consumption by Ohio River sauger.

### Summer

During June through August, age 0 individuals of several prey species reached optimal sizes and became important in sauger diets. Emerald shiners were frequent prey of sauger throughout the year, but peaked in numbers during summer. The faster growing channel catfish and freshwater drum were sizeable portions of the sauger diet only during July and August, similar to the short period of vulnerability observed in other studies (Priegel 1963; Parsons 1971; Krummrich and Heidinger 1973).

Daily ration remained low during June through August, whereas growth in length and weight was also generally reduced. The pattern suggests that temperature was the primary determinant of these rates during summer. Hokanson (1977) cited 22°C as the temperature for optimum growth and consumption for sauger. Water temperatures reached this level in the Ohio River in June, resulting in a relatively short increase in food consumption. During July and August, water temperatures approached the upper incipient lethal temperature of 29–35°C for percids (Hokanson 1977), and sauger probably were not able to find optimal temperatures due to the isothermal nature of the Ohio River. Kichell et al. (1977b), in applying a bioenergetics model to walleye and yellow perch (*Perca flavescens*), indicated that environmental temperatures constitute a major determinant of growth under specified feeding regimes. In the model, allometric relations of food consumption and respiration rates markedly reduced the growth of larger fish as a result of high midsummer water temperatures. The midsummer slump in food consumption by Ohio River sauger during July was probably also related to high temperatures and reduced foraging activity (Forney 1977b; Kitchell et al. 1977b).

### Fall–Winter

Based on maintenance requirements, daily ration levels were sufficient for growth from September to January for Ohio River sauger. The pattern of growth, both in length and weight, closely followed the pattern of food consumption. Nakashima and Leggett (1978) showed similar relationships between growth and food consumption for yellow perch during the major portion of the growing season in Lake Memphremagog, Quebec–Vermont.

Fastest growth for sauger in the Ohio River occurred during October through November and the peak in daily ration occurred in October. Both growth rate and food consumption declined gradually in the November and January samples. These peaks differ from the period of maximum food consumption for walleye in Lake of the Woods, Minnesota, during August and September (Swenson and Smith 1973). The shift of peak ration to later in the fall and continued high growth and food

consumption into winter in the Ohio River probably resulted from different temperature patterns and increased availability of gizzard shad. Water temperatures in the Ohio River exceeded optimal levels for growth and consumption of sauger until after the middle of September (Hokanson 1977).

The period of elevated food consumption by saugers in the Ohio River also corresponded to the first inclusion of large numbers of gizzard shad in the diet. McGee et al. (1977) observed similar increases of threadfin shad (*Dorosoma petenense*) in the diets of sauger during fall and winter in Watts Bar Reservoir, Tennessee. Both threadfin shad and gizzard shad became lethargic and exhibit reduced swimming ability below 10°C (Fitz and Holbrook 1978; Griffith 1978), gizzard shad being more resistant to cold temperatures than threadfin shad (Cox and Coutant 1976). Temperatures below 10°C occurred in the Ohio River during November and January and may have been a factor in the higher consumption of gizzard shad during these months.

Despite small sample sizes, Minton and McLean (1982) observed elevated food consumption during winter by sauger feeding on threadfin shad in Watts Bar Reservoir, Tennessee. Diana (1979) observed much lower daily rations for northern pike during extended periods of low temperatures in Lac Ste Anne, Alberta, where clupeids were not a major prey species. If the correlation between daily food consumption and prey density observed by Swenson and Smith (1976) in Minnesota operates in the Ohio River, the availability of gizzard shad enabled sauger to maintain elevated levels of food consumption through winter.

Levels of growth and food consumption observed overwinter for Ohio River sauger have not been previously observed in other aquatic systems. Minton and McLean (1982) observed elevated levels of food consumption but reduced growth by sauger during winter in Watts Bar Reservoir, Tennessee. No growth in length was observed for these fish from October through February. Adams et al. (1982) suggested that these fish may have been feeding periodically on prey concentrated in warmwater refuges within the reservoir. Other studies of sauger and walleye populations in lakes and reservoirs also have not detected winter growth (Hassler 1957; Kelso and Ward 1972). Work with northern pike from Lac Ste Anne, Alberta, has indicated low rations and minimal growth after October (Diana 1979; Diana and Mackay 1979). In laboratory experiments, Kelso (1972) failed to detect somatic growth of walleye at temperatures below 12°C. Several factors inherent in laboratory situations, including stress and altered prey availability, may have caused the discrepancy between these findings and those observed for sauger in the field. Sauger may also be able to grow at lower temperatures than those determined for walleye. Winter growth and ration should be examined more intensively to determine the generality of patterns observed for Ohio River sauger.

### Predation in Large Rivers

Kitchell et al. (1977a) proposed that the optimum habitat of percid fishes may be defined by the littoral and sublittoral environment in lakes under conditions equivalent to those found in large, temperate rivers. Relationships of this type may explain the many similarities in predator–prey interactions observed between the Ohio River and those previously reported for lakes and other aquatic systems. Physical characteristics of the Ohio River, however, particularly temperature patterns, do appear to have altered predictably patterns of predation by sauger.

Water temperature and its effect on sauger and cold-sensitive prey appear to have been primarily responsible for the patterns of growth and food consumption observed for Ohio River sauger. The annual period of growth and food consumption above maintenance levels was longer and peaked later in the year in the river than in other types of aquatic systems. Previous studies in other large rivers also have indicated longer annual feeding cycles than those present in lakes or reservoirs (Backiel 1971; Griffiths 1976; Popova and Sytina 1977).

The general pattern of bimodal food consumption shown by sauger in the Ohio River has been observed in several lakes (Forney 1977b; Kitchell et al. 1977b; Diana 1979; Doble and Eggers 1978). Reduced feeding during spawning and midsummer declines in food consumption appear to be common for several predators in a variety of aquatic systems. Conversion efficiencies of saugers were also similar to those observed for fishes in other types of aquatic systems. The average conversion efficiencies of sauger throughout the annual cycle (19.7%) and during the growing season (18.1%) were within the range of values summarized by Lane et al. (1979) for a variety of fish species. The similarity between growing season and annual values is the result of the close correspondence between growth and food consumption observed for Ohio River sauger throughout the annual cycle. Conversion efficiencies for Ohio River sauger are similar to those determined for age II and III walleye in Lake of the Woods (Swenson and Smith 1973). Calculations for these walleye were based on estimates made during the growing season. Physical characteristics such as flow did not, as might be expected, increase metabolism and reduce food conversion efficiency for sauger in the Ohio River.

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## References

ADAMS, S. M., R. B. MCLEAN, AND J. A. PARROTTA. 1982. Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. Trans. Am. Fish. Soc. 111: 549–558.

AGGUS, L. A. 1979. Effects of weather on freshwater fish predator–prey dynamics, p. 47–56. *In* H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

ALLEN, K. R. 1969. Distinctive aspects of the ecology of stream fishes: a review. J. Fish. Res. Board Can. 26: 1429–1438.

BACKIEL, T. 1971. Production and food consumption of predatory fish in the Vistula River. J. Fish Biol. 3: 369–405.

CAMPBELL, K. P. 1979. Predation principles in large rivers: a review, p. 181–191. *In* H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

CARLANDER, K. D. 1950. Growth rate studies of saugers, *Stizostedion canadense* (Smith) and yellow perch *Perca flavescens* (Mitchell), from Lake of the Woods, Minnesota. Trans. Am. Fish. Soc. 79: 30–42.

COX. D. K., AND C. C. COUTANT. 1976. Acute cold-shock resistance of gizzard shad, p. 159–161. *In* G. W. Esch and R. W. McFarlane [ed.] Thermal ecology II. ERDA Symposium Series. Energy Research and Development Administration Technical Information Center, Oak Ridge, TN.

DIANA, J. S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). Can. J. Zool. 57: 2121–2127.

1983. An energy budget for northern pike (*Esox lucius*). Can. J. Zool. 61: 1968–1975.

DIANA, J. S., AND W. C. MACKAY. 1979. Timing and magnitude of energy deposition and loss in the body, liver, and gonads of northern pike (*Esox lucius*). J. Fish Res. Board Can. 36: 481–487.

DOBLE, B. D., AND D. M. EGGERS. 1978. Daily feeding chronology, rate of gastric evacuation, daily ration and prey selection in Lake Washington juvenile sockeye salmon (*Oncorhynchus nerka*). Trans. Am. Fish. Soc. 107: 36–45.

EGGERS, D. M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34: 290–294.

ELLIOTT, J. M., AND L. PERSSON. 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47: 977–991.

FITZ, R. B., AND J. A. HOLBROOK II. 1978. Sauger and walleye in Norris Reservoir, Tenn., p. 82–88. *In* R. L. Kendall [ed.] Selected coolwater fishes of North America. Am. Fish. Soc. Spec. Publ. No. 11.

FORNEY, J. L. 1974. Interactions between yellow perch abundance, walleye predation and survival of alternate prey in Oneida Lake. Trans. Am. Fish. Soc. 103: 15–24.

1977a. Reconstruction of yellow perch (*Perca flavescens*) cohorts from examination of walleye (*Stizostedion vitreum vitreum*) stomachs. J. Fish. Res. Board Can. 34: 925–932.

1977b. Evidence of inter- and intraspecific competition as factors regulating walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. J. Fish. Res. Board Can. 34: 1812–1820.

GARDNER, M. B. 1981. Effects of turbidity on feeding rates and selectivity of bluegills. Trans. Am. Fish. Soc. 110: 446–450.

GRIFFITH, J. S. 1978. Effects of low temperature on the behavior and survival of threadfin shad (*Dorosoma petenense*). Trans. Am. Fish. Soc. 107: 63–69.

GRIFFITHS, W. E. 1976. Food and feeding habits of European perch in the Seluyn River, Canterburg, New Zealand. N.Z. J. Mar. Freshwater Res. 10: 417–428.

HASSLER, W. W. 1957. Age and growth of the sauger (*Stizostedion canadense*) in Norris Reservoir, Tennessee. Tenn. Acad. Sci. 32: 55–76.

HOFMANN, P. 1969. Growth of walleyes in Oneida Lake and its relation to food supply. Fed. Aid Fish Wildl. Restoration Proj. F-17-R-13m Job 1-f: 19 p. Ithaca, NY.

HOKANSON, K. E. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board. Can. 34: 1524–1546.

HYNES, H. B. 1973. The ecology of running waters. University of Toronto Press, Downsview,Ont.

JENKINS, R. M. 1979. Predator–prey relations in reservoirs, p. 123–134. *In* H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

KELSO, J. R. M. 1972. Conversion, maintenance, and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet, and temperature. J. Fish. Res. Board Can. 29: 1181–1192.

KELSO, J. R. M., AND F. J. WARD. 1972. Vital statistics, biomass, and seasonal production of an unexploited walleye (*Stizostedion vitreum vitreum*) population in West Blue Lake, Manitoba. J. Fish. Res. Board Can. 29: 1043–1052.

KITCHELL, J. F., M. G. JOHNSON, C. K. MINNS, K. H. LOFTUS, L. GREIG, AND C. H. OLIVER. 1977a. Percid habitat: the river analogy. J. Fish. Res. Board Can. 34: 1936–1940.

KITCHELL, J. F., D. J. STEWART, AND D. WEININGER. 1977b. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1922–1935.

KRUMMRICH, J. T., AND R. C. HEIDINGER. 1973. Vulnerability of channel catfish to largemouth bass predation. Prog. Fish-Cult. 35: 173–175.

LANE, E. D., M. C. S. KINGLEY, AND D. E. THORNTON. 1979. Daily feeding and food conversion efficiency of the diamond turbot: an analysis based on field data. Trans. Am. Fish. Soc. 108: 530–535.

MACLEAN, J., AND J. J. MAGNUSON. 1977. Species interactions in percid communities. J. Fish. Res. Board Can. 34: 1941–1951.

MANN, R. H. K. 1975. Quantitative fish sampling in two hard water rivers in southern England, p. 194–200. *In* R. L. Welcomme [ed.] Symposium on the methodology for the survey, monitoring and appraisal of fishery resources in lakes and large rivers. EIFAC Tech. Pap. (23) Suppl 1.

1976. Observations on the age, growth, reproduction and food of the pike *Esox lucius* in two rivers in southern England. J. Fish Biol. 8: 179–197.

MATHEWS, C. P. 1971. Contribution of young fish to total production of fish in the River Thames near Reading. J. Fish Biol. 3: 157–180.

MCGEE, M. V., J. S. GRIFFITH, AND R. B. MCLEAN. 1977. Prey selection by sauger in Watts Bar Reservoir, Tennessee, as affected by cold-induced mortality of threadfin shad. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 31: 404–411.

MINTON, J. W., AND R. B. MCLEAN. 1982. Measurements of growth and consumption of sauger (*Stizostedion canadense*): implications for fish energetics studies. Can. J. Fish. Aquat. Sci. 39: 1396–1403.

MOLNAR, GY., E. TAMASSY, AND I. TOLG. 1966.The gastric digestion of living predatory fish, p. 151–173. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, England.

NAKASHIMA, B. S., AND W. C. LEGGETT. 1978. Daily ration of yellow perch (*Perca flavescens*) from Lake Memphremagog, Quebec–Vermont, with a comparison of methods for in situ determinations. J. Fish. Res. Board Can. 35: 1597–1603.

NELSON, W. R. 1968. Reproduction and early life history of the sauger in Lewis and Clark Lake. Trans. Am. Fish. Soc. 97: 159–166.

NELSON, W. R., AND C. H. WALBURG. 1977. Population dynamics of yellow perch (*Perca flavescens*), sauger (*Stizostedion canadense*), and walleye (*Stizostedion vitreum vitreum*) in four main stem Missouri River reservoirs. J. Fish. Res. Board Can. 34: 1748–1763.

NIELSEN, L. A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Can. J. Fish. Aquat. Sci. 37: 11–19.

OGLESBY, R. J., C. A. CARLSON, AND J. A. MCCANN. 1972. River ecology and man. Academic Press, New York, NY.

PARSONS, J. W. 1971. Selective food preference of walleye of the 1959 year class in Lake Erie. Trans. Am. Fish. Soc. 100: 474–485.

POPOVA, D. A., AND L. A. SYTINA. 1977. Food and feeding relations of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in various waters of the USSR. J. Fish. Res. Board Can. 34: 1559–1570.

PRESTON, R. H., AND G. E. WHITE. 1978. Summary of Ohio River fishery surveys. EPA 903/9-78-009. Philadelphia, PA.

PRIEGEL, G. R. 1963. Food of walleye and sauger in Lake Winnebago, Wisconsin. Trans.Am. Fish. Soc. 92: 312–313.

RAWSON, M. R., AND R. L. SCHOLL. 1978. Reestablishment of sauger in western Lake Erie, p. 261–265. *In* R. L. Kendall [ed.] Selected coolwater fishes of North America. Am. Fish. Soc. Spec. Publ. No. 11.

REGIER, H. A., V. C. APPLEGATE, AND R. A. RYDER. 1969. The ecology of the walleye in western Lake Erie. Great Lakes Fish. Comm. Tech. Rep. 15.

SEABURG, K. G., AND J. B. MOYLE. 1964. Feeding habits, digestion rates and growth of some Minnesota warm water fishes. Trans. Am. Fish. Soc. 93: 269–285.

STEIGENBERGER, L. W., AND P. A. LARKIN. 1974. Feeding activity and rates of digestion of northern squawfish (*Ptychocheilus oregonensis*). J. Fish Res. Board Can. 31: 411–420.

SWENSON, W. A., AND L. L. SMITH JR. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30: 1327–1336.

1976. Influence of food competition, predation, and cannibalism on walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) populations in Lake of the Woods, Minnesota. J. Fish. Res. Board Can. 33: 1946–1954.

TRAUTMAN, M. B. 1981. Fishes of Ohio. The Ohio State University Press, Columbus, OH.

WAHL, D. H. 1982. Daily ration, feeding periodicity and prey selection of sauger (*Stizostedion canadense*) in the Ohio River. M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA. 101 p.

WHITTON, B. A. 1975. River ecology. University of California Press, Los Angeles, CA.

WILLIAMS, W. P. 1965. The population density of four species of freshwater fish, roach (*Rutilus rutilus* (L.)), bleak (*Alburnus alburnus* (L)), dace (*Leuciscus leuciscus* (L.)) and perch (*Perca fluviatilis* L.), in the river Thames at Reading. J. Anim. Ecol. 34: 173–185.

WINDELL, J. T., J. F. KITCHELL, D. O. NORRIS, AND J. S. NORRIS, AND J. W. FOLTZ. 1976. Temperature and rate of gastric evacuation by rainbow trout, *Salmo gairdneri*. Trans. Am. Fish. Soc. 105: 712–717.

# Responses of Lake Whitefish (*Coregonus clupeaformis*) to Fertilization of Lake 226, the Experimental Lakes Area

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The responses of an unexploited population of lake whitefish (*Coregonus clupeaformis*) to fertilization of Lake 226 (L226), the Experimental Lakes Area, northwestern Ontario, were measured for 4 yr (1973–77). A vinyl sea curtain separated the lake into a northeast (NE) basin, which received P, N, and C additions, and a southwest (SW) basin, which received only N and C additions. Lake whitefish in the NE basin grew faster, had higher coefficients of condition, and had greater recruitment and production than those in the SW basin during the 2nd through 4th yr of fertilization. No differences between basins were detected in annual survival for fish ≥age 1, but survival of age 0 fish was greater in the NE basin. Whitefish production in L226NE averaged twice that in L226SW from the 2nd to the 4th yr of fertilization, though significant variations occurred between years in both the NE and SW populations.

Les réponses d'une population non exploitée de corégones de lac (*Coregonus clupeaformis*) à la fertilisation du lac 226 (L226) de la zone de lacs expérimentaux du nord-ouest de l'Ontario ont été déterminées pendant 4 années (1973–77). Le lac était divisé par un rideau de vinyle en un bassin nord-est, fertilisé par du P, du N et du C, et un bassin sud-ouest ne recevant que du N et du C. Les corégones du bassin nord-est présentaient une croissance plus rapide, des coefficients de condition plus élevés de même qu'un recrutement et une production plus grandes que ceux du bassin sud-ouest au cours de la 2$^{e}$ à la 4$^{e}$ année de fertilisation. Aucune différence du taux de survie annuel des poissons d'âge ⩾ 1 n'a été notée entre les bassins, mais le taux de survie des poissons d'âge 0 était plus important dans le basin nord-est. La production de corégone dans le bassin nord-est était, en moyenne, deux fois supérieure à celle du bassin sud-ouest, ceci de la 2$^{e}$ à la 4$^{e}$ année de fertilisation, mais les deux populations présentaient des variations significatives d'une année à l'autre.

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Intentional fertilization of ponds and lakes to increase fish yield has a long history in both Europe and North America (Swingle and Smith 1939; Juday et al. 1938; Neess 1949; Hasler and Einsele 1948; Maciolek 1954; Weatherley and Nicholls 1955; Nelson 1959; and others). Most of the lake studies concentrated on the responses of stocked populations of young fish. More recently, interest in cultural eutrophication has led to further study of the effects of nutrient enrichment on natural fish populations (Larkin and Northcote 1969; Colby et al. 1972; Nakashima and Leggett 1975). The responses of fish populations to nutrient enrichment have been confounded frequently by other simultaneous perturbations such as exploitation, species addition, or both (Colby et al. 1972; Leach et al. 1977). Other studies have concentrated on responses of young salmonids (Barraclough and Robinson 1972; LeBrasseur et al. 1978; and others), or commenced after enrichment had occurred for many years when fish populations had reached new equilibrium levels (Nakashima and Leggett 1975). Little is known about the responses of a northern fish population, composed largely of older, sexually mature individuals, as described by Johnson (1976), to nutrient addition. The purpose of this study was to evaluate changes in an unexploited population of lake whitefish (*Coregonus clupeaformis*) to increased nutrient loading over the first four years of fertilization in Lake 226, the Experimental Lake Area, northwestern Ontario.

I monitored six population parameters throughout this study: growth, condition, abundance, survival, fecundity, and production. Based on previous lake whitefish literature and previous fertilization studies, I hypothesized that one or more of these parameters would change in response to fertilization. Healey (1975) and Healey and Nichol (1975) showed that lake whitefish growth, survival, and fecundity could vary extensively in unexploited whitefish populations. In addition, Healey (1978, 1980) found that lake whitefish growth, fecundity, and recruitment changed when unexploited populations were experimentally fished. In previous short-term fertilization studies, changes in growth (Weatherley and Nicholls 1955; Haines 1973; and others), survival, and abundance (Nelson and Edmondson 1955; LeBrasseur et al. 1978) were responses. In addition, the responses may change if the fertilization is continued for more than 1 yr (McConnell 1965; Hall et al. 1970).

While earlier studies agreed qualitatively that greater productivity at lower trophic levels led to higher fish yields (Hasler and Einsele 1948; Ball and Tanner 1951; and others), more precise quantifications between trophic levels has occurred more recently (McConnell 1963, 1965; Hall et al. 1970; Sreenivason 1964;

Melack 1976; and others). A secondary goal of this study was to compare lake whitefish production with production at lower trophic levels for 4 yr of lake fertilization.

## Materials and Methods

### Study Site

Lake 226 (L226) is a small lake with two basins located in the Experimental Lakes Area, northwestern Ontario (Cleugh and Hauser 1971). In early June 1973, a vinyl sea curtain was installed to isolate the northeast (NE) (8.3 ha, 14.7 m $Z_{max}$) from the southwest (SW) (7.8 ha, 11.6 m $Z_{max}$) basin. There was no evidence of an independent whitefish population in each basin prior to wall installation, and the wall effectively segregated the L226 whitefish into two nonmixing populations from May 1973 to October 1976 (Mills 1981). The physical characteristics of the two basins were very similar. From 1973 to 1980, phosphorus ($0.34\ g \cdot m^{-2} \cdot yr^{-1}$) was added to L226NE, while both basins received nitrogen (NE 1.81 and SW $1.93\ g \cdot m^{-2} \cdot yr^{-1}$) and carbon (NE 3.46 and SW $3.69\ g \cdot m^{-2} \cdot yr^{-1}$). Further details of the experiment are documented eleswhere (Schindler 1974; Schindler and Fee 1974; Davies 1980; Fee 1980). In general, blue-green algal blooms occurred each year in L226NE; similar blooms did not occur in L226SW. Primary production and dipteran emergence have generally been higher in L226NE than in L226SW during this fertilization period. In addition to lake whitefish the L226 fish fauna consisted of pearl dace (*Semotilus margarita*), fine-scale dace (*Chrosomus neogaeus*), redbelly dace (*Chrosomus eos*), fathead minnow (*Pimephales promelas*), and slimy sculpin (*Cottus cognatus*).

### Field Sampling Procedures

All sampling procedures were selected to minimize mortality of whitefish. Lake whitefish were collected from September 1973 to late October 1977 using trap nets and gill nets. Small-mesh (9.5 mm) deepwater trap nets (Beamish 1972) were alternated between basins at approximately 2- to 3-wk intervals during the May and September–October sampling periods of each year from September 1973 to November 1977, and during the remainder of the ice-free seasons in 1974 and 1975. Nets were lifted in midmorning (08:00–10:30). Ice was used to lower water temperatures in fish-holding containers whenever epilimnetic temperatures were ≥20°C commencing in late summer 1974. Trapnet catches were supplemented during spring and fall with fish caught using multipanel gill nets (11-, 25-, 30-, 33-, 38-, and 45-mm bar mesh) starting in late September 1975 because trapnet catch-per-unit of effort (CPUE) decrease throughout the study. Gill nets were emptied at 15-min intervals to minimize netting mortality, and fish were held overnight prior to sampling to assess short-term gillnetting mortality (which was less than 6%).

Whitefish were anesthetized with MS-222® (tricaine methane sulfonate), weighed, measured (fork length), and during October sampling sexed by extrusion of gametes. Fish ≤26 cm long were batch-marked by clipping two to three rays from different fins systematically for individual sampling periods. The first 161 fish >26 cm caught in L226NE were tagged using Floy® gun tags (Dell 1968). All other fish ≥26 cm were tagged using modified Carlin tags (White and Beamish 1972).

The first two to three rays from the left pelvic fin were removed at initial tagging for age determination. Analogous rays from the other pelvic fin were removed from fish which were recaptured at least one winter after initial tagging to validate the aging technique. Details of the technique used for age determinations are available in Mills and Beamish (1980).

The stomachs of lake whitefish larger than 30 cm trapnetted from May 1974 to May 1976 were pumped (Seaburg 1957) to compare diets between basins and years. Smaller whitefish were not stomach pumped because fish died after sampling. Nets were periodically emptied at 07:00–08:15, 12:00–13:30, and 18:00–20:00 during individual days in July and August 1974 and 1975. Usually, fish stomachs pumped during the latter two periods had empty stomachs. Therefore, only whitefish caught after single overnight sets were sampled to minimize the amount of food scavenged from net bottoms.

### Data Analyses

*Growth*

Growth of whitefish to age 0 and 1 was estimated from mean length at age data collected during fall sampling periods from 1973 to 1976. No lengths were recorded for age 0 fish collected in L226SW during fall 1973. Growth between basins and years was compared using unpaired *t*-tests.

Growth of fish older than 1 was estimated by a combination of back-calculated lengths (1971–76, 2 yr of prefertilization and 4 yr of fertilization) and observations of growth of tagged individuals between successive fall sampling periods. I detected no significant growth retardation due to tagging (K. H. Mills, unpubl. data). Sections from the first pelvic fin ray were used to back-calculate fish lengths using the modified direct proportionality formula of Bagenal and Tesch (1978) after the technique was validated (Mills 1981). Analysis of covariance (Dixon and Massey 1969) was used to compare growth of whitefish between basins for fish ≥age 1 with fish length as the covariate after the data were ln transformed. The assumption of equality of regression slopes for analyses of covariance was tested and no significant differences between basins were detected.

Condition factors ($k$) were calculated for each whitefish caught during this study using the allometric formula of Bagenal and Tesch (1978) with $b = 3.12$ (GM regression) derived from the length–weight relationship among all whitefish caught during this study. Data were stratified by individual age classes and 2.5-cm length classes prior to analyses and stratified by capture method (trap net or gill net).

*Abundance estimates*

Jolly–Seber mark–recapture models (Jolly 1965; Seber 1973) were used to estimate population sizes ($\hat{N}_i$) for L226 whitefish from fall 1973 to fall 1976 using the programs of Arnason and Baniuk (1978). Whitefish data were divided into two strata ( on the basis of fin-ray ages) for each basin: (1) fish ≥age 1 at fall 1973 (year classes 1952–72) and (2) fish age 1 at fall 1974 (1973 year class). Because new recruits ($\hat{B}_i$) were excluded from each stratum, the data satisfied the "death-only" model (i.e. subject to only mortality through time). The 1974 and 1975 year classes in each basin and the 1973 year class in L226SW were very weak; CPUE data were used to compare relative abundances of these year classes between basins and years. Population estimates for age 0 whitefish were not possible.

Each of the four assumptions (no tag loss, equal catchability, equal survival, and the closure assumption) of the Jolly–Seber models were tested following methods described in Seber (1973). These tests and their results are summarized in Mills (1981). Significant tag loss was detected among the gun-tagged

whitefish of stratum 1, and increased mortality was detected for fish released from two sampling periods in each basin. The Jolly–Seber "full" model (which gave $\hat{N}_i$, $\hat{\phi}_i$, and an estimate of new recruits entering the population) was used for the stratum 1 whitefish in L226NE; this model gave unbiased $\hat{N}_i$ and $\hat{\phi}_i$ even when tag loss was occurring (Arnason and Mills 1981). Sampling periods (early summer 1974), where increased mortality of released fish, whether newly tagged or tagged previously, was detected, were omitted from all analyses (Mills 1981). Death-only analyses were used for the stratum 1 fish of L226SW and the stratum 2 fish of L226NE.

While $\hat{N}_1$ (September–October 1973) is not available from the Jolly–Seber full model for L226NE stratum 1 fish (the first estimate available is $\hat{N}_2$), it can be formed in this case as

$$\hat{N}_1 = n_{1g} + N_{1s}$$

where $n_{1g}$ is the known number of fish (161) released with gun tags at time 1 and $\hat{N}_{1s}$ is the death-only model estimated for fish taggd with modified Carlin tags. The standard error (SE) of this $\hat{N}_1$ is simply SE($\hat{N}_{1s}$) because $n_{1g}$ is known exactly and does not contribute to the SE.

*Annual survival rates*

The Jolly–Seber death-only model was used to calculate all survival estimates ($\hat{\phi}_i$) for L226 whitefish. Capture histories for gun-tagged whitefish were excluded from all analyses because the high tag loss rate could bias $\hat{\phi}_i$ (Arnason and Mills 1981). Annual survival was estimated using capture data from successive fall sampling periods, 1973–77, when most fish were caught. To test whether annual survival was related to whitefish age or length, separate $\hat{\phi}_i$ were calculated for four whitefish age groups (1–3, 4–6, 7–10, and 11–25) and three length groups (17–25, 26–30, and 31–45 cm) from the strata 1 and 2 whitefish. Division of age and length groups into smaller intervals was not practical; the precision of the estimates would be very poor. Jolly–Seber models do not allow interstratum movement, so all lengths or ages were converted to those at fall 1973 (using back-calculated lengths or ages), and capture histories were then blocked into the above age or length classes for separate analyses.

*Fecundity estimates*

Female whitefish were gillnetted in 1976 to compare inter-basin fecundity at length. Ovaries were preserved in Gilson's fluid (Bagenal 1967) and total counts were obtained using the dry weight method of Healey and Nichol (1975). Analysis of covariance was used to compare ln fecundities between basins with ln fish fork length (FL) as the covariate. The assumption of homogeneity of regression slopes for analysis of covariance was tested and no significant differences were detected.

*Food analyses*

Stomach contents were preserved in formalin during field sampling and later sorted under a binocular microscope to family for chironomids and chaoborids and to species for cladocerans and copepods. While stomach pumping did not remove all the contents of whitefish stomachs, representative samples were obtained (Mills 1981). Percent composition by number was used for comparisons between basins and years.

*Production estimates*

Production ($P$ in wet weight) of lake whitefish was estimated for each basin from the time of wall installation in early June 1973 to October 1976 using the Chapman (1978) modification of the Ricker method where $P = GB$ ($G$ = instantaneous growth rate, $B$ = the average biomass of two adjacent estimates). Annual production was estimated for each of five age groups (1–3, 4–6, 7–10, 11–15, and 16–25) between successive fall sampling periods from October 1973 to October 1976, and from early June 1973 to October 1973. Population estimates for each group were obtained from the sum of (1) mark–recapture $\hat{N}_i$ for the 1952–72 year classes smoothed by eye and (2) proportionality estimates for the 1973–76 year classes (except the 1973 year class in L226NE, where mark–recapture estimates were used). An indirect method was used to derive population estimates for June 1973. The average monthly survival rate from October 1973 to October 1976 (0.867) for fish of the 1952–72 year classes was applied to the fall 1973 population estimates to obtain a June estimate for each basin:

$$\hat{N}_i \text{ June} = \frac{\hat{N}_i \text{ October 1973}}{0.867^5}.$$

These abundance estimates were based on the assumption that mortality was constant through time in L226. To determine if mortality was constant within years, whitefish $\hat{N}_i$ for the 1952–72 year classes for each basin were plotted with their standard errors as a function of time (in months). A logarithmically decreasing relationship between estimates and time was evident, consistent with the hypothesis of constant monthly survival.

Estimates of gain in fish weight from the beginning to the end of a growth period were calculated by converting growth in length to that in weight using the length–weight relationship for the population from 1973 to 1976 ($\ln \text{wt} = 3.12 \times \ln \text{FL}$, $r = 0.978$, $N = 1559$).

## Results and Discussion

### Growth and Condition

Fish growth is generally viewed as a very sensitive response indicator to nutrient enrichment (e.g. Nikolsky 1963; Smith 1969; Vinberg and Lyakhnovich 1969; Hall et al. 1970; Haines 1973). Growth of L226NE whitefish was greater in L226NE than in L226SW the 2nd through 4th yr of fertilization for fish ≥age 1. No significant differences were detected between mean lengths of age 0 fish between basins or years (Table 1). Age 1 fish in L226NE were significantly longer ($t$-test, $P < 0.05$) than age 1 fish in L226SW in 1974. Too few fish from the 1974 and 1975 year classes were captured at age 0 and age 1 to make other comparisons between years and basins possible. Because growth of older, larger whitefish was correlated more with fish length ($r = 0.908$) than age ($r = 0.745$) for the years 1971–76, growth was summarized with fish length as the covariate. The same data plotted with age as the covariate showed similar trends. Growth of older, larger whitefish was not significantly different between basins in 1973 ($P > 0.15$, Fig. 1), but white-

TABLE 1. Mean fork length (mm) at age for whitefish age 0 and 1 in fall samples 1973, 1974, and 1976 (95% confidence intervals indicated in parentheses).

| Age class | Year | Age | L226NE | $N$ | L226SW | $N$ |
|---|---|---|---|---|---|---|
| 1973 | 1973 | 0 | 92.0 (±2.4) | 37 | — | — |
| | 1974 | 1 | 182.4 (±2.0) | 74 | 173.3 (±6.7) | 22 |
| 1976 | 1976 | 0 | 93.7 (±2.7) | 29 | 90.8 (±2.4) | 14 |

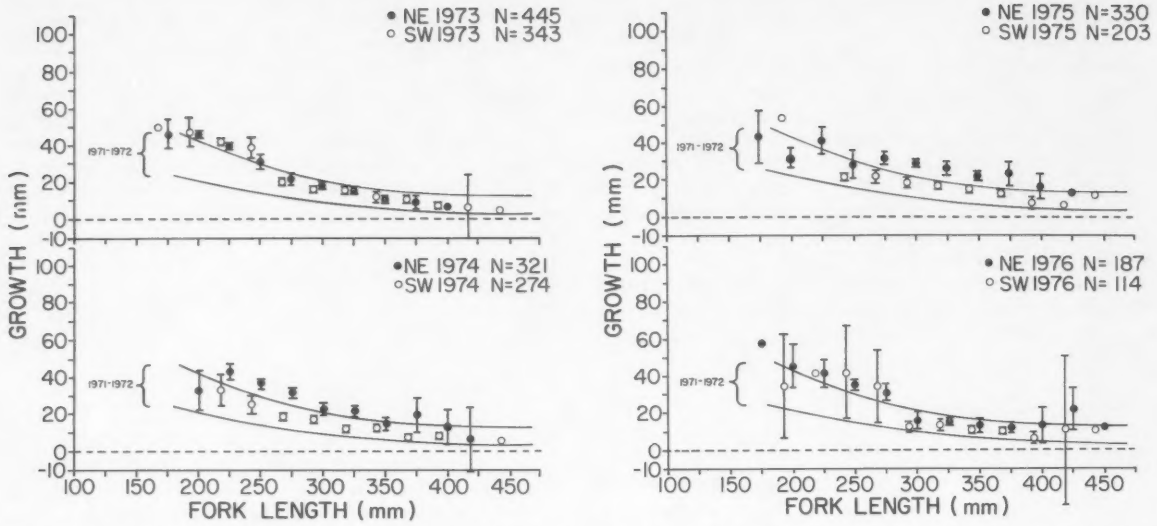


FIG. 1. Growth of lake whitefish ≥age 1 for 4 yr of fertilization in L226NE and L226SW. Means and 95% confidence intervals are plotted for 25-mm length groups. The range of whitefish growth for 1971 ($N = 471$) and 1972 ($N = 693$), drawn from means and 95% confidence intervals for 25-mm length groups, is also presented.

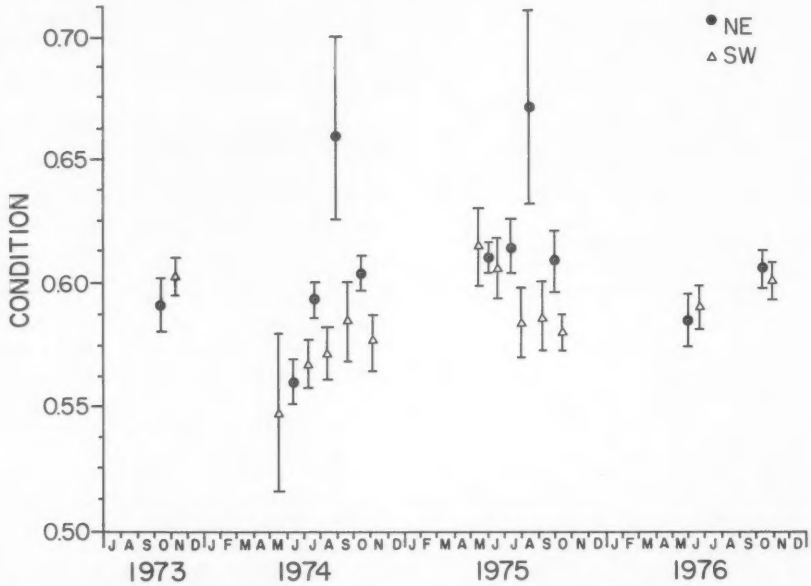


FIG. 2. Condition of L226 whitefish from 1973 to 1976. Mean condition and 95% confidence intervals for each sampling period are plotted.

fish growth was significantly greater ($P < 0.01$) in L226NE during than 2nd (1974) through 4th yr (1976) of fertilization. Differences in growth between basins were most pronounced in 1975, averaging 1.4 cm·fish$^{-1}$ greater in L226NE than in L226SW each year. Differences were less pronounced in 1976, averaging 0.8 cm·fish$^{-1}$ greater in L226NE.

In addition to differences between basins, whitefish growth differed between years. The best growth in each basin was 1975, followed by 1974, 1973, and then 1976. Annual growth in L226SW for each year of fertilization, 1973–76, was very similar to growth in 1971 and 1972. Growth of L226NE whitefish was greater each year, 1974–76, than prewall yearly growth, but 1973 growth was well within the 1971 and 1972 range. The 1975 growth season was the year of fastest growth in this basin, followed by 1974 and 1976. In general, annual variations were most pronounced in sexually mature (>27 cm, ≥age 4–5) fish.

No trends existed between whitefish length, age, or capture method and condition for any of the sampling periods (K. H. Mills, unpubl. data; Mills 1981). Therefore, data for individual

age and length groups were combined for presentation here (Fig. 2). No significant interbasin differences in condition were detected for 1973 or 1976 ($t$-tests, $P > 0.05$), but L226NE whitefish had higher condition factors than L226SW basin fish for much of 1974 and 1975. Condition usually peaked in August of each year for L226NE, and significant differences ($t$-tests, $P < 0.05$) continued to fall sampling periods. The years of greatest growth differences between basins, 1974 and 1975, were also the years when the greatest condition difference between basins occurred.

While the increased growth of the younger fish in L226NE is not surprising, the response of older, sexually mature fish has not been documented previously. Many other studies with stocked immature trout (Ball 1948; Weatherley and Nicholls 1955; Smith 1969), or with young sockeye salmon (Nelson 1959; LeBrasseur et al. 1978), have shown similar results. Pond fertilization studies (Maciolek 1954; Vinberg and Lyakhnovich 1969; Hall et al. 1970) were almost always conducted with stocked populations of young, immature fish. The response of older, sexually mature whitefish in L226NE was as striking as the response of younger fish in 1974 and 1975. Some fish, which showed very poor growth for the 3–5 yr prior to fertilization, as judged by annuli on fin-ray sections, responded with 1 yr of growth equal to the previous 3–5. Others (Colby et al. 1972; Leach et al. 1977) have speculated that this had occurred for other species in lakes with increased nutrient input.

## Abundance Estimates

More whitefish were present in L226NE than L226SW throughout the first 4 yr of fertilization (Table 2). Only estimates for fall sampling periods are presented here; estimates for spring and summer sampling periods are presented in Mills (1981) along with details of the calculations. The 1973 year class was very abundant in L226NE, almost equalling the combined 1952–72 year classes. This year class was very abundant in both basins in 1973 (Fig. 3). The 1974 and 1975 year classes were very small in each L226 basin, contributing to the decreasing number of lake whitefish >age 1 in each basin from 1973 to 1976. This decrease is slightly misleading because abundant young-of-the-year whitefish were plentiful in each basin in 1976 (Fig. 3). The vinyl curtain apparently did not disrupt spawning activities of lake whitefish; the appearance of strong and weak year classes coincided between basins. Two consecutive year class failures, 1974 and 1975, are unusual, but also occurred in 1966 and 1967 prior to wall installation (Mills 1981).

## Annual Survival

Annual survival rates of whitefish were not significantly different either between basins or years (Table 3). Almost all $\hat{\phi}_i$ were within 1 SE of other estimates whether they were based on all capture histories or stratified by age or length groups. The average annual survival of whitefish from the first stratum (≥age 1) was 0.74 for L226NE and 0.76 for L226SW. This was very similar to the L226 catch curve survival rate, $0.73 \pm 0.04$ (95% confidence interval), based on fin-ray ages for the fall 1973 catch in both basins (Mills and Beamish 1980). This catch curve rate can be viewed as an average survival in L226 for a number of years prior to fertilization. Therefore, there was no evidence for change in annual survival for fish >age 1 in either basin.

While no significant differences in annual survival between basins occurred for large, older whitefish, differences did occur between basins for the 1973 year class. The 1973 year class had an average annual survival of 82% from 1974 to 1976 (Table 3). While no analogous analysis was possible for the L226SW 1973 year class, some inferences can be made based on trapnet CPUE data (Fig. 3). There was a dramatic decline (73%) in the catch rate of the L226SW 1973 year class between fall 1973 (age 0)

TABLE 2. Population estimates for fall sampling periods for L226NE and L226SW. Estimates do not include age 0 fish.

| Year | Basin | Year classes | Number (SE) | Total |
|---|---|---|---|---|
| 1973 | NE | 1952–72 | 677 (33) | 677 |
| | SW | 1952–72 | 504 (37) | 504 |
| 1974 | NE | 1952–72 | 510 (59) | 914 |
| | | 1973 | 404 (31) | |
| | SW | 1952–72 | 386 (26) | 451 |
| | | 1973 | 75 | |
| 1975 | NE | 1952–72 | 376 (36) | 682 |
| | | 1973 | 302 (48) | |
| | | 1974 | 4 | |
| | SW | 1952–72 | 318 (23) | 344 |
| | | 1973–74 | 26 | |
| 1976 | NE | 1952–72 | 235 (19) | 451 |
| | | 1973 | 202 (33) | |
| | | 1974–75 | 14 | |
| | SW | 1952–72 | 198 (20) | 223 |
| | | 1973–75 | 25 | |

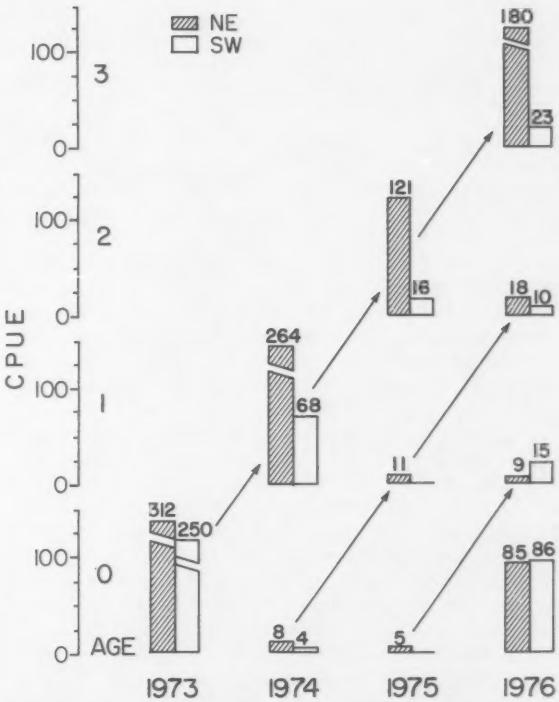


FIG. 3. Trapnet CPUE for the 1973–76 lake whitefish year classes in L226NE and L226SW during fall sampling periods. CPUE were adjusted to 100 trapdays.

TABLE 3. Annual survival estimates for L226 whitefish from the Jolly–Seber death-only model (SE in parentheses). Gun-tagged animals were deleted prior to analyses in L226NE. $N$ = number of capture histories used to form estimates. All estimates are for fish from the 1952–72 year classes, except where otherwise noted.

| | Basin | 1973–74 | 1974–75 | 1975–76 | $N$ |
|---|---|---|---|---|---|
| Total | NE | 0.84 (0.12) | 0.66 (0.10) | 0.71 (0.10) | 296 |
| | SW | 0.76 (0.09) | 0.87 (0.10) | 0.64 (0.08) | 288 |
| Age in 1973 | | | | | |
| 0[a] | NE | —[b] | 0.78 (0.17) | 0.85 (0.23) | 336 |
| 1–3 | NE | 0.88 (0.23) | 0.55 (0.15) | 0.75 (0.15) | 160 |
| | SW | —[c] | —[c] | 0.55 (0.15) | 60 |
| 4–6 | NE | —[c] | —[c] | 0.72 (0.20) | 37 |
| | SW | —[c] | —[c] | 0.87 (0.24) | 28 |
| 7–10 | NE | 0.87 (0.23) | 0.72 (0.20) | 0.68 (0.20) | 59 |
| | SW | —[c] | —[c] | 0.63 (0.10) | 101 |
| 11–25 | NE | 0.76 (0.24) | 0.74 (0.27) | 0.82 (0.31) | 40 |
| | SW | 0.63 (0.13) | 0.87 (0.15) | 0.72 (0.18) | 92 |
| Length (mm) in 1973 | | | | | |
| 176–250 | NE | 0.97 (0.27) | 0.74 (0.27) | 0.82 (0.31) | 40 |
| | SW | 0.63 (0.13) | 0.87 (0.15) | 0.72 (0.18) | 92 |
| 251–300 | NE | 0.66 (0.17) | 0.68 (0.19) | 0.72 (0.18) | 91 |
| | SW | —[c] | —[c] | 0.49 (0.11) | 92 |
| 301–425 | NE | 0.82 (0.16) | 0.71 (0.15) | 0.92 (0.25) | 58 |
| | SW | 0.61 (0.11) | 0.97 (0.13) | 0.64 (0.10) | 46 |

[a]Based on mark–recapture data for the 1973 year class.
[b]No estimate available.
[c]Inadmissible estimate, $\hat{\phi}_i > 1.0$, or biased by adjacent $\hat{\phi}_i > 1.0$.

and fall 1974 (age 1). The decline in the catch rate of the L226NE whitefish over the same period was 15%. The higher mortality rate of the 1973 year class in L226SW may have continued from fall 1974 to fall 1975 (age 2) when there was a further 77% decline, but this decline may be biased by the relatively low catches of the 1973 year class in both basins in 1975. The catch rate in each basin increased from 1975 to 1976. Based on these data, the 1973 year class in L226SW underwent a significantly higher annual loss rate than the analogous year class in L226NE.

While these results are somewhat preliminary, it appears that lake whitefish mortality in L226 varies only in younger age groups, ages 0–2, and is relatively constant after this period. The relatively constant survival rate of adult fish between years is consistent with observations of Bell et al. (1977) for Lesser Slave Lake, Alberta, although immature fish had slightly higher survival than adults. While changes in survival are not generally believed to be a major response mechanism in pond fertilization studies (Vinberg and Lyakhnovich 1969; Hall et al. 1970; Dobbins and Boyd 1976), others have found either a positive correlation between year class strengths of salmon and nutrient enrichment of lakes (Nelson and Edmondson 1955; Mathieson 1972) or an inverse correlation between survival of young-of-the-year and nutrient status (Nakashima and Leggett 1975). In each case where a response has occurred, it has occurred in very young fish.

## Fecundity

No significant differences ($P > 0.25$) in total fecundity at length for individual fish were detected between basins for 1976. There were no consistent differences between basins for either small, relatively young females or older, larger fish. Fecundities at length were very similar to those reported by Healey and Nichol (1975) and Healey (1978). While Healey (1978) found that lake whitefish responded to exploitation by increased fecundity at length, this did not occur in response to increased nutrient input in L226NE.

While there were no differences in whitefish fecundities between basins for whitefish of similar lengths, total fecundity of the whitefish population in L226NE was probably greater than in L226SW. This was an indirect result of the faster growth in L226NE from 1974 to 1976. For example, utilizing the relationship between fecundity and length for L226 whitefish (Mills 1981), a L226NE female whitefish first reaching sexual maturity in 1973 at a fork length of 30 cm (age 6) would increase in length and fecundity to ~32 cm (8000 eggs) in 1974, ~35 cm (11 500 eggs) in 1975, and ~36 cm (13 000 eggs) in 1976. A L226SW female whitefish of similar size in 1973 would be ~31 cm (6500 eggs), ~33 cm (9000 eggs), and ~34 cm (9700 eggs) in succeeding years.

## Stomach Analyses

Despite the small sample sizes, it was obvious that the most important food items in L226NE and L226SW whitefish diets were chaoborids and chironomids (Table 4). While the numbers of cladocerans and copepods in whitefish stomachs were fairly high in July and August 1974 in L226NE, chironomids and chaoborids were ~70% by volume in these samples. Cladocerans and copepods were relatively undigested compared with chironomids, where many times only head capsules could be identified clearly. *Latonia setifera* and *Euryptus lamillatus* were the major cladocerans and *Mesocyclops edax* and *Diatomus minutus* were the major copepods in whitefish stomachs. Other minor components in the diet were leeches, adult dipterans, and small clams.

TABLE 4. Percent composition by number of lake whitefish stomach contents by taxonomic group for L226NE and L226SW basins. $N$ = number of stomachs examined for each sampling period.

| | Chaoborids | Chironomids | Cladocerans | Copepods | Other | $N$ |
|---|---|---|---|---|---|---|
| L226NE | | | | | | |
| Sept. 1973 | 11 | 89 | 0 | 0 | 0 | 8 |
| June 1974 | 39 | 56 | 2 | 2 | 1 | 51 |
| July 1974 | 13 | 47 | 21 | 3 | 16 | 13 |
| Aug. 1974 | 7 | 49 | 24 | 19 | 1 | 12 |
| Sept. 1974 | 14 | 86 | 0 | 0 | 0 | 16 |
| June 1975 | 37 | 61 | 2 | 0 | 0 | 21 |
| July 1975 | 30 | 69 | 0 | 0 | 1 | 7 |
| Aug. 1975 | 45 | 54 | 1 | 0 | 0 | 8 |
| Sept. 1975 | 11 | 89 | 0 | 0 | 0 | 16 |
| June 1976 | 4 | 94 | 0 | 0 | 2 | 16 |
| L226SW | | | | | | |
| July 1974 | 38 | 62 | 0 | 0 | 0 | 13 |
| Aug. 1974 | 12 | 88 | 0 | 0 | 0 | 11 |
| Oct. 1974 | 15 | 83 | 0 | 0 | 2 | 22 |
| June 1975 | 26 | 73 | 0 | 0 | 1 | 14 |
| Aug. 1975 | 19 | 81 | 0 | 0 | 0 | 8 |
| Oct. 1975 | 32 | 67 | 1 | 0 | 0 | 9 |

TABLE 5. Summary of production estimates for L226NE and L226SW whitefish (kg) with estimates of average production for individual fish of each age class (g) in parentheses. Estimates are calculated between successive fall sampling periods, except 1973 (May to September–October). The average biomass was the mean of biomass present at the start and end of each yearly period.

| | 1973 | | 1974 | | 1975 | | 1976 | |
|---|---|---|---|---|---|---|---|---|
| Age | NE | SW | NE | SW | NE | SW | NE | SW |
| 1–3 | 23.7 | 13.6 | 32.2 | 9.8 | 32.0 | 4.6 | 22.3 | 1.8 |
| | (70.5) | (80.0) | (79.7) | (69.6) | (64.6) | (47.1) | (72.9) | (64.2) |
| 4–6 | 4.5 | 3.1 | 5.3 | 2.2 | 16.5 | 7.7 | 8.3 | 3.8 |
| | (54.9) | (48.4) | (76.7) | (43.9) | (92.2) | (59.9) | (43.3) | (40.8) |
| 7–10 | 7.8 | 6.5 | 10.6 | 6.2 | 8.2 | 5.4 | 3.8 | 3.5 |
| | (56.1) | (50.1) | (85.2) | (49.0) | (97.5) | (68.9) | (59.0) | (47.2) |
| 11–15 | 2.1 | 6.1 | 5.2 | 4.8 | 6.0 | 5.4 | 2.3 | 2.7 |
| | (44.7) | (47.3) | (77.4) | (35.2) | (109.7) | (57.3) | (66.7) | (36.2) |
| 16–25 | 0.2 | 1.1 | 0.3 | 1.1 | 1.0 | 1.6 | 1.3 | 1.5 |
| | (14.3) | (40.7) | (45.4) | (32.0) | (82.5) | (38.8) | (61.3) | (29.3) |
| Total | 38.3 | 30.4 | 53.6 | 24.1 | 63.7 | 24.7 | 38.1 | 13.3 |
| Total $g \cdot m^{-2}$ | 0.46 | 0.38 | 0.64 | 0.31 | 0.77 | 0.32 | 0.46 | 0.17 |
| Average biomass (kg) | 130.2 | 146.7 | 235.1 | 176.3 | 206.0 | 151.8 | 178.6 | 126.1 |

## Production Estimates and Their Relation to Lower Trophic Levels

Whitefish production in L226NE was consistently higher ($\bar{X}$ = 48.4 $kg \cdot yr^{-1}$) than in L226SW ($\bar{X}$ = 23.1 $kg \cdot yr^{-1}$) from 1973 to 1976, though the annual totals varied from 38.1 to 63.7 kg for L226NE and from 13.3 to 30.4 kg for L226SW (Table 5, details of calculations are located in Mills 1981). Production of L226NE whitefish was approximately 20% higher than L226SW whitefish in 1973. Subsequently, whitefish production in L226NE was more than twice the production in L226SW from the 2nd to 4th yr of fertilization.

The large differences in whitefish production between basins from 1974 to 1976 were largely attributable to the increased survival of the 1973 year class in L226NE, and to the differences in individual growth between basins from 1974 to 1976. Over 56% of the total whitefish production in L226NE from 1974 to 1976 was due to age 1–3 fish, while only 27% of the total production in L226SW was due to this age group during the same period. The 1973 year class dominated this age 1–3 group in both basins. In addition, production of older fish was also greater in L226NE than in L226SW from 1974 to 1976. For fish ≥age 7, production was over 40 $g \cdot fish^{-1} \cdot yr^{-1}$ greater in L226NE than in L226SW during 1974 and 1975, and over 20 $g \cdot fish^{-1} \cdot yr^{-1}$ greater in 1976.

While age 0 fish were not included in production estimates, this probably did not bias comparisons between basins. Catches of young-of-the-year fish were similar between basins for each year from 1973 to 1976 (Fig. 3). The whitefish production estimates were probably underestimates for 1973 and 1976 because abundant young-of-the-year were not included in the calculations.

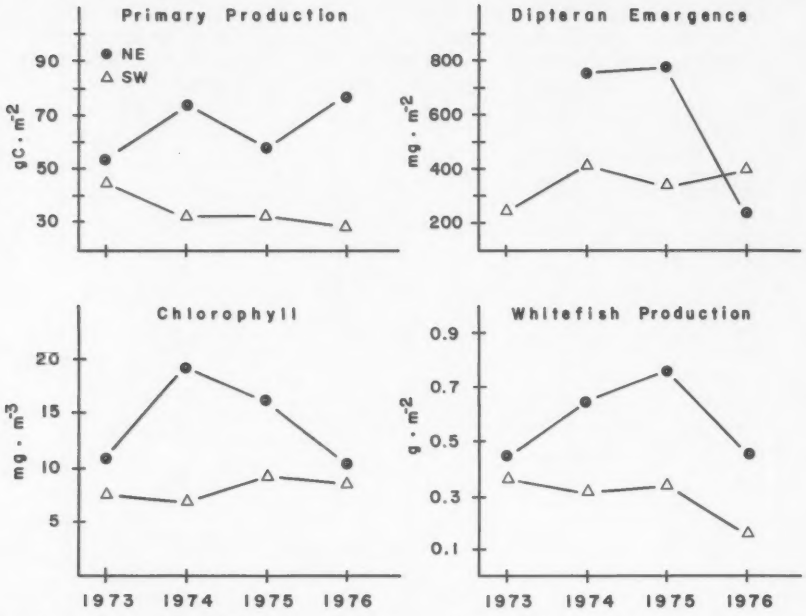


FIG. 4. Annual average epilimnetic chlorophyll concentrations, primary production, dipteran emergence, and lake whitefish production for L226 from 1973 to 1976. Chlorophyll concentrations are from D. W. Schindler (Freshwater Institute, unpubl. data); primary production data are from Fee (1980); dipteran emergence data are from I. J. Davies (Freshwater Institute, unpubl. data).

Fish production or commercial fishery yield often has been correlated with primary production or chlorophyll concentrations (e.g. Hall et al. 1970; Melack 1976; Hrbáček 1969), benthic production or biomass (e.g. Gerking 1962; Hall et al. 1970), or zooplankton production and biomass (e.g. Smith 1969; Hall et al. 1970). The L226 experiment is unique because primary production (Fee 1979), epilimnetic chlorophyll concentrations (D. W. Schindler, Freshwater Institute, Winnipeg, Man., unpubl. data), dipteran emergence (Davies 1980), and lake whitefish production have been measured over a series of years (Fig. 4). As in other studies, there was generally a good correlation between average epilimnetic chlorophyll concentrations and annual whitefish production in L226NE and L226SW from 1973 to 1976 ($r = 0.86$, $P < 0.01$, $N = 8$), or between dipteran emergence and whitefish production ($r = 0.77$, $P < 0.05$, $N = 8$). The relationship between whitefish production and primary production was not as pronounced, but still significant ($r = 0.67$, $P < 0.05$, $N = 8$). If a 1-yr lag was incorporated between primary production and whitefish production, the correlation improved ($r = 0.90$, $P < 0.01$, $N = 6$). Similar "use lags" (McConnell 1963) have been described previously (Vinberg and Lyakhnovich 1969; Lellack 1965; and others) and attributed to the time needed for conversion of dead algae to benthic biomass. Additional data for these four parameters for later years of fertilization may show use lags more clearly.

While the levels of nutrient enrichment for both basins were constant from year to year, the responses of algae, dipterans, and lake whitefish varied extensively. This is not surprising for L226NE where phosphorus input was substantially increased. A sudden increase in nutrient loading may put a lake into nutrient disequilibrium, and a number of years of sustained additions (or reductions) are necessary before a new equilibrium is reached. A new total phosphorus level in L226NE would probably be reached after 4–6 yr of fertilization (D. W. Schindler, pers. comm.; Mills 1981), with only a relatively small response the 1st yr (16–26%). Therefore, it is not surprising that there was little or no response of the whitefish population the 1st yr of fertilization. This lag in response of fish populations to whole lake fertilization was probably a major factor for the inconsistent results of earlier lake fertilizations (Maciolek 1954; Wagner and Parker 1973), which were conducted for 1 or 2 yr. During the years of detectable response to phosphorus additions in L226NE, 1974–76, lake whitefish biomass averaged 33% higher in L226NE than in L226SW (Table 3). It is unlikely that lake whitefish production and biomass had reached a new equilibrium after 4 yr of fertilization.

## Conclusion

I monitored six population parameters for lake whitefish throughout 4 yr of fertilization in each L226 basin: growth, condition, abundance, survival, fecundity, and production. The whitefish in L226SW apparently did not respond to nitrogen and carbon fertilization. Growth and survival were similar to estimates prior to wall installation and fertilization, and the whitefish biomass in L226SW was relatively constant for the 4 yr. These results are consistent with many other pond and lake fertilization studies that have shown that increased fish production occurred only when phosphorus additions accompanied nitrogen (Juday et al. 1938; Neess 1949; Maciolek 1954; Vinberg and Lyakhnovich 1969). The whitefish in L226NE responded to phosphorus, nitrogen, and carbon additions with greater growth, condition, and survival of age 0 whitefish. The growth response was most pronounced the 2nd and 3rd yr of fertilization. In addition to greater growth in length for these

years, whitefish were heavier (had higher condition) than fish of the same size in L226SW. Increased survival of age 0 fish in L226NE led to a higher abundance of lake whitefish in L226NE than in L226SW. The higher condition and greater growth of age 0 fish in L226NE may be responsible for their increased survival; these results are consistent with the observations of Nelson and Edmondson (1955) and Mathieson (1972) for salmon. Nikolsky (1963) cited other examples of positive correlations between fish survival and condition. In spite of greater growth and higher condition, I could detect no change in annual survival of whitefish >age 1 in L226NE.

The increased growth and higher condition of L226NE whitefish was apparently due to an increase in their primary prey items, chironomids and chaoborids, which in turn was related to an increase in their food supply, as indicated by increased chlorophyll and primary production. While the whitefish biomass was relatively static in L226SW for the 4 yr (Table 5), it increased in L226NE. While one might conclude that the decrease in whitefish growth, condition, production, and biomass in L226NE in 1976 might signal that the whitefish population had reached a new equilibrium after 4 yr of fertilization, the total phosphorus data indicated that a higher equilibrium level may not be reached for at least two additional years.

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## References

ARNASON, A. N., AND L. BANIUK. 1978. POPAN-2: a data maintenance and analysis system for mark–recapture data. Charles Babbage Research Centre, St. Pierre, Man. 269 p.

ARNASON, A. N., AND K. H. MILLS. 1981. The bias and loss of precision due to tag loss in Jolly–Seber estimates for mark–recapture experiments. Can. J. Fish. Aquat. Sci. 38: 1077–1095.

BAGENAL, T. B. 1967. A short review of fish fecundity, p. 89–112. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

BAGENAL, T. B., AND F. W. TESCH. 1978. Age and growth, p. 101–136. *In* T. B. Bagenal [ed.] Methods for assessment of fish production in freshwaters, 3rd ed. Blackwell Scientific Publications, Oxford.

BALL, R. C. 1948. Fertilization of natural lakes in Michigan. Trans. Am. Fish. Soc. 78: 145–155.

BALL, R. C., AND H. TANNER. 1951. The biological effects of fertilizer on a warm-water lake. Mich. State Coll. Agric. Exp. Stn. Tech. Bull. 223: 32 p.

BARRACLOUGH, W. E. AND D. ROBINSON. 1972. The fertilization of Great Central Lake. III. Effect on juvenile sockeye salmon. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 70: 37–48.

BEAMISH, R. J. 1972. Design of a trapnet for sampling shallow water habitats. Fish. Res. Board Can. Tech. Rep. 305: 14 p.

BELL, G., P. HANDFORD, AND C. DIETZ. 1977. Dynamics of an exploited population of lake whitefish (*Coregonus clupeaformis*). J. Fish. Res. Board Can. 34: 942–953.

CHAPMAN, D. W. 1978. Production in fish populations, p. 5–25. *In* S. D. Gerking [ed.] Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford.

CLEUGH, T. R., AND B. W. HAUSER. 1971. Results of the initial survey of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 123–128.

COLBY, P. J., G. R. SPANGLER, D. A. HURLEY, AND A. M. MCCOMBIE. 1972. Effects of eutrophication on salmonid communities in oligotrophic lakes. J. Fish Res. Board Can. 29: 975–983.

DAVIES, I. J. 1980. Relationships between dipteran emergence and phytoplankton production in the Experimental Lakes Area, northwestern Ontario. Can. J. Fish. Aquat. Sci. 37: 523–533.

DELL, M. B. 1968. A new fish tag and rapid cartridge fed applicator. Trans. Am. Fish. Soc. 97: 57–59.

DIXON, W. J., AND F. J. MASSEY, JR. 1969. Introduction to statistical analysis. McGraw-Hill Inc., New York, NY. 638 p.

DOBBINS, D. A., AND C. E. BOYD. 1976. Phosphorus and potassium fertilizer of sunfish ponds. Trans. Am. Fish. Soc. 105: 536–540.

FEE, E. J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. Limnol. Oceanogr. 24: 401–416.

1980. Important factors for estimating annual phytoplankton production in the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. 37: 513–522.

GERKING, S. D. 1962. Production and food utilization in a population of blue gill sunfish. Ecol. Monogr. 32: 31–78.

HAINES, T. A. 1973. Effects of nutrient enrichment and a rough fish population (carp) on a game fish population (smallmouth bass). Trans. Am. Fish. Soc. 102: 346–354.

HALL, D. J., W. E. COOPER, AND E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 25: 839–928.

HASLER, A., AND W. EINSELE. 1948. Fertilization for increasing productivity of natural inland waters. Trans. 13th N. Am. Wildl. Conf.: 527–551.

HEALEY, M. C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. 32: 427–448.

1978. Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 35: 945–950.

1980. Growth and recruitment of experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. Can. J. Fish. Aquat. Sci. 37: 255–267.

HEALEY, M. C., AND C. W. NICOL. 1975. Fecundity comparisons for various stocks of lake whitefish, *Coregonus clupeaformis*. J. Fish. Res. Board Can. 32: 404–407.

HRBÁČEK, J. 1969. Relations between some environmental factors and fish yield as basis for a predictive model. Verh. Int. Ver. Limnol. 17: 1069–1081.

JOHNSON, L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. 33: 2459–2488.

JOLLY, G. M. 1965. Explict estimates from capture–recapture data with both death and immigration — stochastic model. Biometrika 52: 225–247.

JUDAY, C., C. L. SCHLOEMER, AND C. LIVINGSTONE. 1938. Effect of fertilizers on plankton production and fish growth in a Wisconsin lake. Progr. Fish-Cult. 40: 24–27.

LARKIN, P. A., AND T. G. NORTHCOTE. 1969. Fish as indicators of eutrophication, p. 256–273. *In* Eutrophication: causes, consequences, correctives. Proceedings of an International Symposium on Eutrophication held at Madison, Wisconsin, 1967. National Academy of Sciences, Washington, DC.

LEACH, J. H., M. G. JOHNSON, J. R. M. KELSO, J. HARTMAN, W. NÜMANN, AND B. ENTZ. 1977. Responses of percid fishes and their habitats to eutrophication. J. Fish. Res. Board Can. 34: 1964–1971.

LEBRASSEUR, R. J., C. D. MCALLISTER, W. E. BARRACLOUGH, W. D. KENNEDY, J. MANZER, D. ROBINSON, AND K. STEPHANS. 1978. Enhancement of sockeye salmon (*Oncorhynchus nerka*) by lake fertilization in Great Central Lake: summary report. J. Fish. Res. Board Can. 35: 1580–1596.

LELLACK, J. 1965. The food supply as a factor regulating the population dynamics of bottom animals. Mitt. Int. Ver. Limnol. 13: 128–138.

MACIOLEK, J. A. 1954. Artificial fertilization of lakes and ponds. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 113: 41 p.

MATHIESON, O. A. 1972. Biogenic enrichment of sockeye salmon lakes and stock productivity. Verh. Int. Ver. Limnol. 18: 1089–1095.

MCCONNELL, W. J. 1963. Primary productivity and fish harvest in a small desert impoundment. Trans. Am. Fish. Soc. 92: 1–12.

1965. Relationship of herbivore growth to rate of gross photosynthesis in microcosms. Limnol. Oceanogr. 10: 539–543.

MELACK, J. M. 1976. Primary productivity and fish yields in tropical lakes. Trans. Am. Fish. Soc. 105: 575–580.

MILLS, K. H. 1981. The responses of a lake whitefish (*Coregonus clupeafor-*

*mis*) population to whole-lake fertilization. Ph.D. thesis, University of Manitoba, Winnipeg, Man. 209 p.

MILLS, K. H., AND R. J. BEAMISH. 1980. Comparison of fin-ray and scale age determinations for lake whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. Can. J. Fish. Aquat. Sci. 37: 534–544.

NAKASHIMA, B. S., AND W. C. LEGGETT. 1975. Yellow perch (*Perca flavescens*) biomass responses to different levels of phytoplankton and benthic biomass in Lake Memphremagog, Quebec–Vermont. J. Fish. Res. Board Can. 32: 1785–1797.

NEESS, J. C. 1949. Development and status of pond fertilization in central Europe. Trans. Am. Fish. Soc. 76: 335–358.

NELSON, P. R. 1959. Effects of fertilizing Bare Lake, Alaska, on growth and production of red salmon (*O. nerka*) U.S. Fish. Wildl. Serv. Fish. Bull. 60: 59–86.

NELSON, P. R., AND W. T. EDMONDSON. 1955. Limnological effects of fertilizing Bare Lake, Alaska. U.S. Fish. Wildl. Serv. Fish. Bull. 56: 416–436.

NIKOLSKY, G. V. 1963. The ecology of fishes. Academic Press, New York, NY. 352 p.

SCHINDLER, D. W. 1974. Eutrophication and recovery in Experimental Lakes: implications for lake management. Science (Wash., DC) 184: 897–899.

SCHINDLER, D. W., AND E. J. FEE. 1974. Experimental Lakes Area: whole lake experiments in eutrophication. J. Fish. Res. Board Can. 31: 937–953.

SEABURG, K. G. 1957. A stomach sampler for live fish. Prog. Fish-Cult. 19: 137–139.

SEBER, G. A. F. 1973. Estimation of animal abundance and related parameters. Griffin, London. 506 p.

SMITH, M. W. 1969. Fertilization and predator control to increase growth rate and yield of trout in a natural lake. J. Fish. Res. Board Can. 25: 2011–2036.

SREENIVASON, A. 1964. The limnology, primary production, and fish yield in a tropical pond. Limnol. Oceanogr. 9: 391–396.

SWINGLE, H., AND E. SMITH. 1939. Increasing fish production in ponds. Trans. 4th N. Am. Wild. Conf.: 332–338.

VINBERG, G. G., AND V. P. LYAKNOVICH. 1969. Fertilization of fish ponds. Fish. Res. Board Can. Transl. Ser. 1339: 482 p.

WAGNER, J. F., AND M. PARKER. 1973. Primary production and limiting nutrients in a small, sub-alpine Wyoming lake. Trans. Am. Fish. Soc. 102: 698–706.

WEATHERLEY, A., AND A. G. NICHOLLS. 1955. The chemical enrichment of a lake. Aust. J. Mar. Freshwater Res. 6: 443–468.

WHITE, W. J., AND R. J. BEAMISH. 1972. A simple fish tag suitable for long-term marking experiments. J. Fish. Res. Board Can. 29: 339–341.

# Responses of Benthic Macroinvertebrate Species to Manipulation of Interstitial Detritus in Carnation Creek, British Columbia

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Culp, J. M., and R. W. Davies. 1985. Responses of benthic macroinvertebrate species to manipulation of interstitial detritus in Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. 42: 139–146.

Experimental manipulations were conducted in Carnation Creek, British Columbia, to determine the response of macroinvertebrate distribution and abundance to differences in detritus source and quantity. Four treatments (no detritus, low hemlock (*Tsuga heterophylla*), low alder (*Alnus rubra*), high alder) with a standardized substrate were established in a riffle and left for 28 d. Densities and/or biomasses of 12 of the 20 colonizing macroinvertebrate taxa were significantly different among the detritus treatments. Microbial activity, detritus processing, and macroinvertebrate abundances were highest in substrate patches with alder detritus. Compared with the no detritus and low hemlock treatments, the low alder treatment increased the abundances of nine taxa and decreased three taxa, while the high alder treatment increased the abundances of six taxa and decreased six taxa. Thus, detritus source and quantity strongly influenced macroinvertebrate community composition within the streambed. Although most of the macroinvertebrates in all treatments were either collector–gatherer or shredder detritivores, these macroinvertebrates responded to changes in detritus in a species-specific manner. Therefore, the Carnation Creek experiments emphasize the importance of interstitial detritus in the substrate as a factor that influences the microdistribution of the benthos at the species, rather than trophic feeding, assemblage level.

Des expériences ont été effectuées dans le ruisseau Carnation (Colombie-Britannique) afin de déterminer les réponses de la distribution et de l'abondance des macroinvertébrés à la présence de détritus d'origine et de quantité variables. Quatre conditions (absence de détritus, faible quantité de tsuga (*Tsuga heterophylla*) et quantités faible et élevée d'aulne de l'Orégon (*Alnus rubra*) sur substrat normalisé) ont été établies pendant 28 jours sur un haut-fond. Les densités et/ou biomasses de 12 des 20 taxons de macro invertébrés ayant colonisé les substrats différaient de façon significative en fonction des conditions. L'activité microbienne, la transformation des détritus et l'abondance des macroinvertébrés étaient les plus importantes dans les zones de substrat portant les détritus d'aulnes. Comparativement aux conditions « absence de détritus » et « faible quantité de tsuga », la faible quantité d'aulne a provoqué une augmentation de l'abondance de neuf taxons et la diminution de celle de trois autres, tandis que la condition « quantité d'aulne élevée » s'est traduite par un accroissement de l'abondance de six taxons et par la diminution de celle de six autres. L'origine et la quantité des détritus influaient donc fortement sur la composition de la communauté des macroinvertébrés du lit du cours d'eau. La plupart des macroinvertébrés présents dans toutes les conditions étaient des détritivores de types cueilleurs-récolteurs ou déchiqueteurs, mais ces ceux-ci n'en n'ont pas moins réagi aux détritus d'une façon particulière à l'espèce. Les essais effectués au ruisseau Carnation soulignent donc l'importance des détritus interstitiels du substrat comme facteur influant sur la microdistribution du benthos au niveau des espèces plutôt qu'au niveau trophique.

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Particulate organic matter derived from terrestrial leaf litter can comprise a significant proportion of the energy budgets of low-order streams (sensu Strahler 1957) draining catchment basins of northern temperate forests (Minshall 1967; Fisher and Likens 1973). In these streams the benthic macroinvertebrate communities can play an important role in the processing of leaf litter and other particulate organic matter (Anderson and Sedell 1979), as the trophic compositions of these communities are often dominated by shredder and collector detritivores. Although shredders and collectors forage upon different particle sizes of detritus (Cummins 1974), detritus utilization by both guilds (sensu Root 1967; Jaksie 1981) is affected by the source (i.e. leaf type) of the organic matter (Anderson and Sedell 1979; Cummins and Klug 1979) and its standing crop of microbial biomass (Ward and Cummins 1979). Leaves that undergo rapid microbial colonization may be selected by shredders (Iverson 1973; Kaushik and Hynes 1971), presumably due to the nutritional importance of the microbial biomass (Ward and Cummins 1979; Cummins and Klug 1979). Thus, the biomass of microbes on the detritus, detritus quantity (Culp et al. 1983), and detritus particle size all potentially affect the composition of detritivore guilds.

Previous studies have demonstrated that leaf packs on the surface of the streambed affect shredder detritivore distribution (Egglishaw 1964, 1969; Peterson and Cummins 1974; Sedell et al. 1975; Reice 1974, 1980). Given equivalent times of conditioning (i.e. leaching and microbial colonization; Sedell et al. 1975), shredders select packs composed of leaves that are conditioned faster and have higher microbe biomass, rather than more slowly processed leaves (Cummins and Klug 1979). Similar generalizations have not been made for collector–gatherers, although members of this guild often colonize leaf

packs with fast processing rates in high densities (Peterson and Cummins 1974; Anderson and Sedell 1979).

Although the responses of the benthos to patches of large particulate detritus at the streambed surface have often been recorded, few investigators (Egglishaw 1964; Rabeni and Minshall 1977; Peckarsky 1980) have attempted to manipulate detritus within substrate interstices, even though many macroinvertebrates forage within these interstices. Experimental manipulations of interstitial detritus must quantify the source, amount, and microbial conditioning of the detritus as in surface leaf pack experiments. However, only the study by Peckarsky (1980) meets these experimental design requirements. In the manipulations of both Egglishaw (1964) and Rabeni and Minshall (1977), unknown proportions of medium (MPOM; 0.25–1 mm) and large (LPOM; 1–16 mm) particulate organic matter were mixed, and the source and microbial conditioning of the detritus was not measured. Clearly, in all these studies, LPOM was the dominant detrital component, and their results relate to shredder detritivores that preferentially colonized the LPOM. These investigations did not test the quantitative effects of MPOM manipulation on collector–gatherers that forage on these detritus particles.

Our experiment examined whether interstitial organic detritus directly influenced lotic macroinvertebrate community composition and structure in the absence of differences of stone substrate composition. The experimental manipulation is the counterpart to work that established that macroinvertebrate colonization was not affected by substrate particle size and heterogeneity when interstitial detritus was standardized (Culp et al. 1983). We also demonstrated that the presence of detritus significantly affected detritivore microdistribution. Here we report how changes in the quantity and source of interstitial detritus in a standardized stony substrate affect macroinvertebrate distribution and abundance. Unlike previous field manipulations, these detritus treatments included quantified amounts of MPOM and LPOM.

## Study Area

Carnation Creek is a third-order stream flowing into Barkley Sound on the west coast of Vancouver Island, British Columbia, and is in the Coastal Western Hemlock (*Tsuga heterophylla* (Bong.)) biogeoclimatic zone (Klinka et al. 1979). The discharge and temperature regimes, water chemistry, and salmonid species composition of the stream have been described by Stockner and Shortreed (1976). The experimental riffle (1.6 m length × 2.3 m width) was located 10 m above the main discharge gauging station and 0.6 km above the estuary. Riparian vegetation along this stream reach was primarily composed of red alder (*Alnus rubra* Bong.), salmonberry (*Rubus spectabilis* Pursh), salal (*Gaultheria shallon* Pursh), and occasionally large trees of western hemlock, Sitka spruce (*Picea sichensis* Bong.), or western redcedar (*Thuja plicata* Donn).

## Materials and Methods

Standardized substrates were inoculated with four detritus treatments to determine whether interstitial detritus directly influenced the distribution and abundance of macroinvertebrates: (ND) no detritus; (LH) low hemlock detritus (62.5 g/m$^2$); (LA) low alder detritus (62.5 g/m$^2$); and (HA) high alder detritus (125 g/m$^2$). Standing crop of detritus in the stream was 54 ± 12 g/m$^2$, thus, treatments LH and LA received slightly more than ambient quantities of detritus, while treatment HA had twice as much as LH and LA. Additionally, these detritus levels cover the range used in previous detritus manipulation experiments (e.g. Egglishaw 1964; Minshall and Minshall 1977; Rabeni and Minshall 1977; Peckarsky 1980).

Detritus was obtained by collecting alder leaves which had a physical appearance similar to autumn shed leaves from trees felled 5 wk earlier, and by shaking brown needles from hemlock branches. These leaves and needles were conditioned separately for 5 wk in the absence of invertebrates and sunlight in containers that were continuously flushed with stream water (Culp et al. 1983). Each conditioned detritus type was shredded in a blender and wet sieved into medium (230–850 μm) and large (850 μm – 2.0 mm) particulate organic matter fractions.

Substrate composition in the experimental treatments was standardized by collecting large gravel (9.5–16.0 mm) and small pebbles (16.0–31.5 mm) from dry areas of the streambed, as in treatment GP of Culp et al. (1983), and combining the two in a 1:1 volumetric mixture. Subsequently, each detritus treatment was produced by placing the appropriate detritus with a medium to large ratio fixed at 2:1 along with the standardized substrate in cylindrical plastic containers (0.008 m$^2$, 10 cm diameter, 6.5 cm deep; five replicates per treatment). The sides of each container had two 230-μm mesh windows (3 × 10 cm) to allow water flow through the substrate. Gravel and pebbles of the experimental size ranges with visually similar periphyton growth were collected from an upstream riffle and used as the top layer of each container. The containers were temporarily sealed with lids to prevent loss of detritus while they were imbedded 6.5 cm into the experimental riffle with the upper edge level with the streambed surface. When the containers were in place, the lids were removed and current velocity 2.5 cm above each container was measured with a Pygmy Gurley meter. Discharge was continuously monitored during the experiment by Environment Canada.

After 4 wk (29 July to 26 August 1980) the containers were resealed, gently lifted from the streambed, and the community respiration of each container measured in the laboratory (Fig. 1). Subsequently, the detritus and invertebrates were preserved in 10% formalin. All macroinvertebrate samples were subsampled before the animals were separated from the detritus under 12× magnification following the protocol of Wrona et al. (1982), identified to the lowest possible taxon, and counted. After identification, each taxon was dried for 24 h at 60°C and weighed with a Cahn 25 automatic electrobalance (±0.001 mg). The detritus from each container was wet sieved and the ash-free dry mass determined for the small (SPOM; 106–230 μm), medium (MPOM; 230–850 μm), and large (LPOM; 850 μm–2 mm) particulate organic matter size fractions. The accumulated organic and inorganic sediments in treatment ND, which initially contained only gravel and pebbles, were used to indicate whether natural sedimentation had altered the detritus in treatments LH, LA, and HA.

To determine the impact of detritivore feeding upon the original 2:1 MPOM to LPOM detritus ratio, five containers identical to treatment LA were immersed in formalin (treatment F) to prevent biological processing and imbedded immediately downstream of the other treatments. This procedure was repeated every 5 d for treatment F, and the MPOM:LPOM ratio for treatment F was measured again after 28 d and compared with the ratios of treatments LH, LA, and HA. Losses of detritus

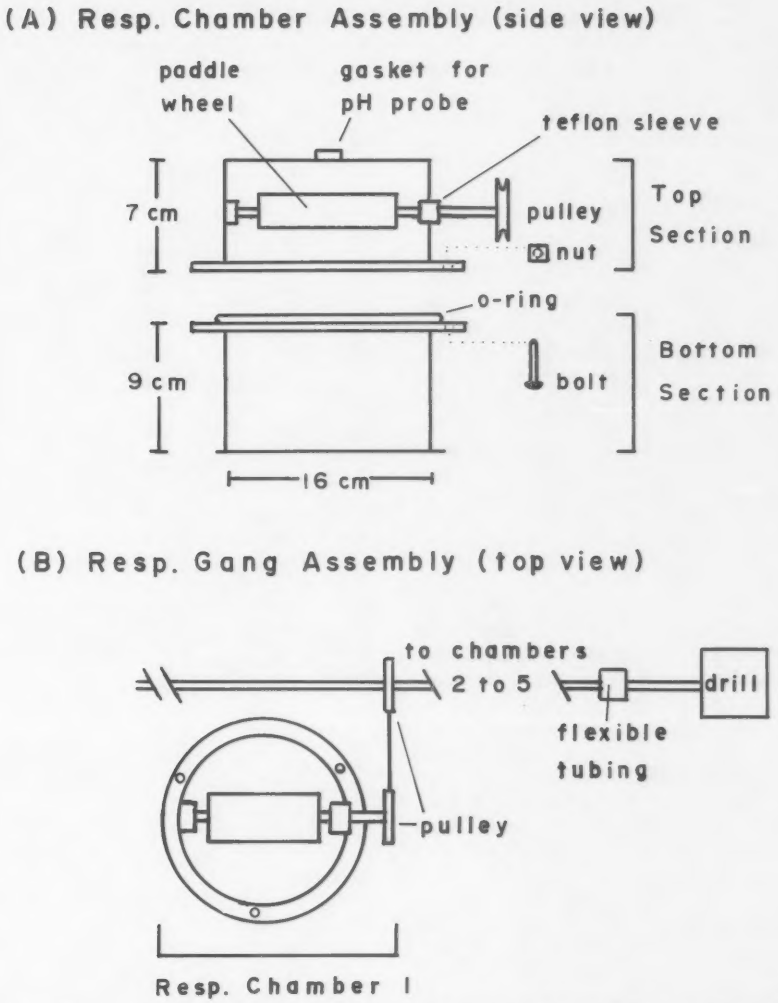


FIG. 1. Community respirometer assembly showing the (A) side view of the top and bottom sections of the respirometer and (B) top view of the respirometer gang assembly.

during the processes of removal from and replacement into the streambed were minimized by temporarily sealing these containers with lids as outlined above.

### Laboratory Community Respiration Technique

The respiration chamber consisted of a bottom container made of PVC piping, a Plexiglas plate used for covering the bottom section in the field, and a Plexiglas top section containing a brass paddle wheel turned by a variable speed drill via a pulley system (Fig. 1). In the field, each substrate container was inserted into the watertight bottom section and sealed to minimize disturbance during transport (0.5 km in 20 min) to the laboratory. In the laboratory, each chamber was placed in a water bath at ambient creek temperature, the cover removed, and the top section of the respirometer fitted over the bottom ensuring that no air bubbles were inside the chambers. A pH probe was inserted through a gasket seal in the top section, and pressure differences were equalized by inserting a syringe needle (18 gauge) through a Vacutainer septum seal. The water bath was covered with black plastic, the paddle wheel was started (100 rpm) to prevent vertical stratification, and a 1-h acclimation period was begun to allow primary production to cease (Hargrave 1969). After this period, pH was recorded every 10 min for 1 h using a Fisher Accumet model 620 meter equipped with a five-probe capacity, Fisher model 157 switchbox, and glass electrodes. Changes in pH were converted to the release of $CO_2$ (milligrams per litre) using the equations of Vollenweider (1969). Note that community respiration could not be assessed for treatment F because the pH probes would not function properly in the presence of formalin.

### Statistical Methods

The null hypotheses for the experiment were that density and biomass (transformed to log $(x + 1)$, Elliott 1977), community respiration, detritus between 106 and 230 μm (SPOM), and current velocity were not significantly different among detritus

treatments ND, LH, LA, and HA. Each hypothesis was tested by employing a model I ANOVA (Zar 1974). If the hypothesis was rejected, the Student–Newman–Keuls (SNK) multiple range test (Zar 1974) was used to establish the significantly dissimilar treatments. Hypothesis rejection for each analysis was set at the $p = 0.05$ probability level.

## Results

### Environmental Conditions

During the experimental period the average daily water temperature ranged from 13 to 15°C, pH from 6.9 to 7.3, and total alkalinity from 16.3 to 21.2 mg $CaCO_3$/L. Current velocity throughout the experimental riffle was similar (20–31 cm/s) and no significant differences were recorded between the treatments. Mean daily discharge was also relatively constant (42–62 L/s) during the experiment, and at these levels of discharge, movement of inorganic sediments was restricted to silt and clay particles. Thus, inorganic sedimentation was only 159 ± 23 mg per container (<0.001% by mass), and similar for all treatments.

### Detritus Manipulations

Because the experimental containers were open at the streambed surface and below the surface via the mesh windows, organic sediments transported from upstream could accumulate in the experimental containers. However, treatment ND, which initially had no detritus, accumulated <7.5 g/m$^2$ (60 mg per container) of detritus over the 28-d experimental period (Fig. 2). This organic sediment was composed largely of filamentous chlorophytes and was distributed almost equally between three particle size classes: 106–230 μm, 230–850 μm, and 850–2000 μm. Clearly, this small quantity of detritus that settled throughout the experimental riffle did not override the much higher manipulated levels of detritus in treatment F, LH, LA, or HA (Fig. 2). Furthermore, the detritus retained in treatments F, LH, LA, and HA was reasonably assumed to be that of the initial manipulative addition as detritus from alder leaves, hemlock needles, or filamentous chlorophytes were easily distinguished.

The sum of the medium (230–850 μm) and large (850–2000 μm) detritus present in each of treatments F, LH, LA, and HA at the end of the experiment represents 79–85% of the original manipulated detritus amounts (Table 1), and subtraction of the organic sedimentation estimate discounts these values only by 2–3%. This sum, however, masks the independent changes of each size fraction. For example, in the LA and HA treatments, 53–61% of the original large detritus was retained, while considerably more of the large detritus (79–82%) was retained in treatments F and LH (Table 1). This trend was reversed for the medium detritus fraction, such that treatments LA and HA had 92–97% of the original quantities of medium particles, and treatments F and LH only 79–81% (Table 1). Differences in the amounts of medium and large detritus retained caused the medium to large detritus ratio of treatments LA and HA to increase from the standardized value of 2:1 to 3.4:1 and 3.2:1 respectively, but in treatments F and LH, the original 2:1 ratio was maintained (Table 1; Fig. 2). Detritus particles <230 μm were not included in the medium to large ratio calculations, since this size class was not initially present in the treatments. By the end of the experiment, significant differences in the amount of the 106–230 μm SPOM size fraction were found between the treatments (Fig. 2). Treatments LA and HA had the greatest amounts of SPOM detritus, while in treatments F and LH, the amounts were similar to the level attributable to organic sedimentation (i.e. treatment ND).

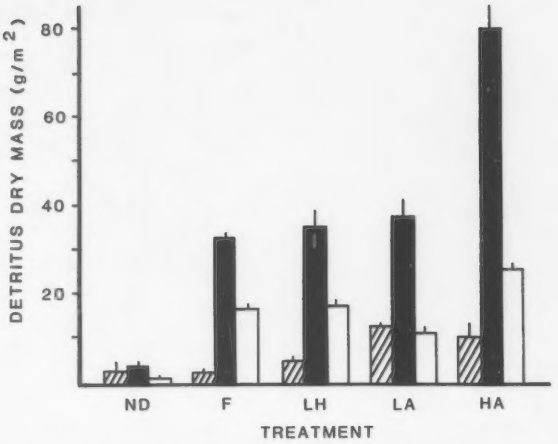


FIG. 2. Dry mass of the large (white), medium (black), and <230 μm (cross-hatched) detritus at the end of the experiment in the no detritus (ND), formalin (F), low hemlock (LH), low alder (LA), and high alder (HA) treatments with SE bars.

TABLE 1. Medium to large detritus ratio of each treatment at the end of the experiment, and the percentage of the total detritus (large + medium fractions), medium detritus, and large detritus retained in the F, LH, LA, and HA treatments expressed as a proportion of the original amount of detritus present.

| | F | LH | LA | HA |
|---|---|---|---|---|
| Total original detritus (medium + large) | 79 | 81 | 79 | 85 |
| Medium detritus MPOM | 79 | 81 | 92 | 97 |
| Large detritus LPOM | 79 | 82 | 53 | 61 |
| Medium to large ratio after experiment | 2:1 | 2:1 | 3.4:1 | 3.2:1 |

The experimental treatments were colonized by a total of 34 macroinvertebrate taxa of which 14 were omitted from the analyses because they had mean densities of <1 individual per treatment. The total density of the remaining 20 taxa pooled was significantly different between the detritus treatments, and SNK tests indicated the LA treatment had higher densities than treatments ND, LH, and HA (Fig. 3). Total macroinvertebrate biomass was also significantly affected by the detritus manipulation, with values in the LA and HA treatments significantly greater than treatments ND and LH (Fig. 3).

Of the 20 taxa present in densities adequate for meaningful analysis, ANOVA indicated that 12 taxa had significantly different densities and/or biomasses among the treatments. For the Ephemeroptera, *Baetis hageni* and *Cinygmula ramaleyi*, the presence of alder detritus in amounts equivalent to ambient detritus levels (treatment LA) increased densities and biomasses relative to treatments ND and LH (Fig. 4; Table 2; Appendix). In the HA treatment, the abundances of these species were significantly decreased below the values in treatments ND and LH (Fig. 4; Table 2; Appendix). Generally, the Chironomidae showed a less complex response to the presence of alder detritus because, as compared with treatments ND and LH, the LA and HA treatments increased the abundances of six chironomid taxa (Fig. 5; Table 2; Appendix) and generally decreased the abun-

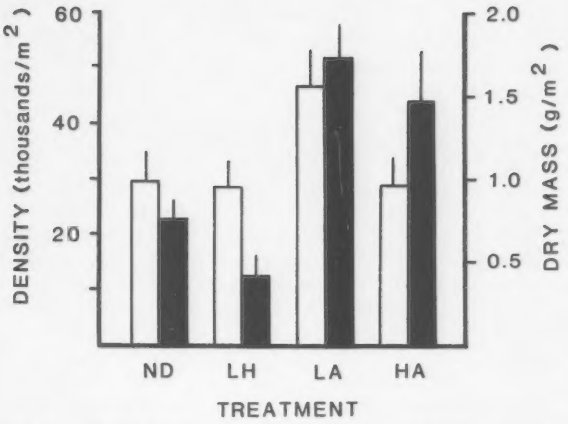


FIG. 3. Total macroinvertebrate density (white) and biomass (black) in the ND, LH, LA, and HA treatments with SE bars.

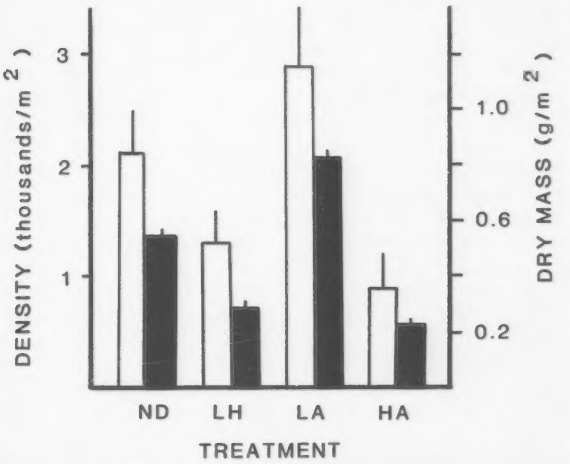


FIG. 4. Ephemeroptera density (white) and biomass (black) in the ND, LH, LA, and HA treatments with SE bars.

dances of three taxa (*Corynoneura*, *Synorthocladius*, *Thienemanniella*) (Fig. 6; Table 2; Appendix). *Orthocladius* was the only chironomid that followed the more complex response to alder detritus exhibited by *B. hageni* and *C. ramaleyi* (Table 2; Appendix). Therefore, compared with treatments ND and LH, treatment LA significantly increased the abundances of nine taxa and decreased three taxa, while treatment HA increased the abundances of six taxa and decreased six taxa (Table 2).

The remaining 8 of the 20 taxa analyzed were either Ephemeroptera (*Cinygmula reticulata*, *Paraleptophlebia*, *Ameletus*, *Ephemerella inermis*, *Baetis tricaudatus*) or Plecoptera (*Alloperla*, *Skwala*, *Zapada cinctipes*), and were not significantly affected by the detritus treatments. Nevertheless, they tended generally to exhibit the patterns of biomass and density shown by the Ephemeroptera (Fig. 4).

Absolute community respiration was significantly different between the treatments, with respiration in treatments ND ($0.17 \pm 0.03$ mg $CO_2 \cdot L^{-1} \cdot h^{-1}$) and LH ($0.18 \pm 0.02$ mg $CO_2 \cdot L^{-1} \cdot h^{-1}$) significantly lower than the values for treatments LA ($0.25 \pm 0.03$ mg $CO_2 \cdot L^{-1} \cdot h^{-1}$) and HA ($0.33 \pm 0.02$ mg $CO_2 \cdot L^{-1} \cdot h^{-1}$). Since the absolute respiration value for treatment ND represents the respiration attributable to the organic sediments plus that of the gravel and pebble substrate, the estimate of treatment ND was subtracted from the above values for treatments LH, LA, and HA to determine the amount of community respiration attributable only to the added hemlock or alder detritus. These values were then standardized per gram of detritus, and they indicate that community respiration was an order of magnitude lower on hemlock detritus (0.02 mg $CO_2 \cdot h^{-1} \cdot g$ detritus$^{-1}$) compared with the alder detritus in treatment LA (0.20 mg $CO_2 \cdot h^{-1} \cdot g$ detritus$^{-1}$) or HA (0.19 mg $CO_2 \cdot h^{-1} \cdot g$ detritus$^{-1}$). Additionally, the standardization showed that

TABLE 2. Summary of the Student–Newman–Keuls tests indicating detritus treatments with significantly different macroinvertebrate density and/or biomass. The LA and HA detritus treatments either increased (+) or decreased (−) macroinvertebrate abundance relative to the ND and LH treatments. ns (ANOVA) = not significant.

| | Alder detritus effect | | | |
|---|---|---|---|---|
| | Density | | Biomass | |
| Taxa | LA | HA | LA | HA |
| Ephemeroptera | | | | |
| *Cinygmula ramaleyi* | + | − | + | − |
| *Baetis hageni* | + | − | + | − |
| Chironomidae | | | | |
| *Brillia* | + | + | + | + |
| Chironomidae pupae | ns | ns | + | + |
| *Micropsectra* | + | + | + | + |
| *Thienemannimyia* group | + | + | ns | ns |
| *Parametriocnemus* | + | + | + | + |
| *Polypedilum* (*Polypedilum*) | + | + | + | + |
| *Orthocladius* | + | − | + | − |
| *Corynoneura* | − | − | − | − |
| *Synorthocladius* | − | − | ns | ns |
| *Thienemanniella* | − | − | ns | ns |

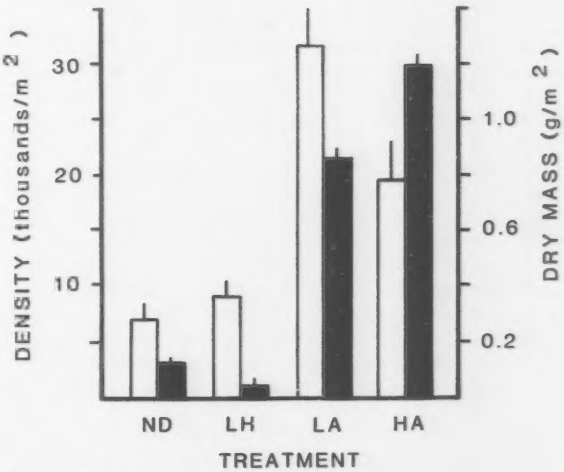


FIG. 5. Chironomid taxa that, relative to the ND and LH treatments, exhibited higher densities (white) and biomasses (black) in the LA and HA treatments with SE bars.

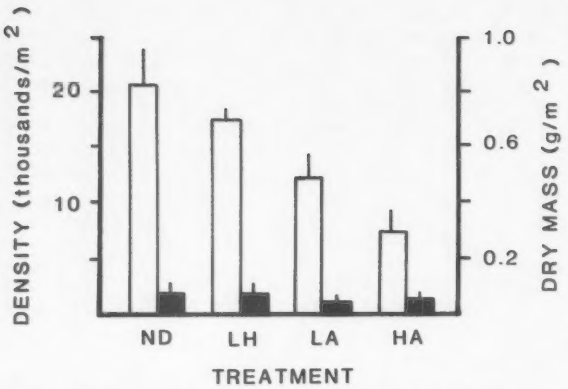


FIG. 6. Chironomid taxa that, relative to the ND and LH treatments, exhibited lower densities (white) and/or biomasses (black) in the LA and/or HA treatments with SE bars.

respiration per gram of detritus was similar in both LA and HA treatments.

## Discussion

During the annually recurring period of low discharge (June–August) within which our experiment was conducted, current velocities throughout stream reaches in Carnation Creek are uniformly low. Minimal transport of sediments by suspension or saltation is characteristic of low discharge levels, and therefore, natural sedimentation did not significantly affect the initial detritus treatments. Since the experimental design of the treatments standardized for intrasubstrate current velocity, substrate particle size and interstitial space, detritus particle size, and detritus conditioning time (Culp et al. 1983), we can verify that source and quantity of detritus were the major differences among the treatments throughout the experiment.

As well as reducing the movement of natural sediments, the low discharge levels also prevented the standardized detritus from being scoured out of the experimental containers with only 15–20% of the added detritus lost from the experimental treatments. These trends suggest that detritus particles within natural substrate patches may move infrequently during periods of low discharge in streams such as Carnation Creek. Throughout periods of low discharge when substrate and detritus patch stability is high, there is clearly the opportunity for macroinvertebrates to restrict their foraging activities for an extended period to a patch of detritus or among adjacent patches.

Because the detritus was retained in the experimental containers, relative estimates of LPOM and MPOM processing by the macroinvertebrate detritivores could be made for treatments F, LH, LA, and HA. Since treatment F measured the loss of detritus due solely to abiotic processes, any significant deviations from the trends of treatment F by treatment LH, LA, or HA can be attributed to biological processing. Thus, it is evident that biological processing of hemlock was negligible during the experiment, as the loss of LPOM and MPOM in treatment LH was similar to that in treatment F. However, the alder treatments lost a greater percentage of LPOM than can be attributed to abiotic losses alone, indicating that LPOM of alder was fragmented into MPOM. This biological fragmentation is directly or indirectly performed either by macroinvertebrate detritivores (Anderson and Sedell 1979) or microbes. Because scouring in the experimental containers was minimal, the MPOM produced from the standardized LPOM of alder by biotic processing appears to have remained in the experimental containers of the LA and HA treatments. This enrichment of MPOM in the alder treatments was approximately equal to the amount of MPOM lost through abiotic processes (Table 1), and since LPOM was converted to MPOM, the MPOM:LPOM ratio in the LA and HA treatments increased to 3.4:1 and 3.2:1, respectively. Biological fragmentation also increased the amount of SPOM in the LA and HA treatments, and future studies should attempt to determine the importance of this size fraction to macroinvertebrate community composition.

The higher rate of fragmentation of alder detritus compared with detritus from hemlock corresponds with the significantly higher biomasses and/or densities of macroinvertebrate detritivores that colonized the LA and HA treatments. Alder detritus can be rapidly processed by detritivores (Anderson and Sedell 1979), and even poorly conditioned leaves can stimulate detritivore growth (Anderson and Grafius 1975). In Carnation Creek the higher levels of biological fragmentation and increased community metabolism (an indicator of microbial activity) per gram of alder detritus, compared with hemlock detritus, suggest that the distribution and abundance of collector–gatherer and shredder detritivores within the streambed was affected by the nutritional value of the detritus food resource (Appendix). Peterson and Cummins (1974), Reice (1978; 1980), and others have demonstrated a similar trend for shredders that colonize LPOM leaf packs on the surface of the streambed.

Our data indicate that microbial activity and macroinvertebrate colonization on hemlock detritus were not significantly different from the ND treatment, although the hemlock had been conditioned for 5 wks and the quantity of detritus in treatment LH equaled that of the LA treatment. Sedell et al. (1974) established that leaf packs of hemlock needles may need long-term (20–25 wk) conditioning before significant processing by macroinvertebrates occurs. This relatively long time period of conditioning suggests that hemlock detritus may be transported a considerable distance downstream before being biologically processed. Although hemlock input into Carnation Creek can be high (Neaves 1978), the frequent floods that occur between September and May potentially could remove much of the hemlock detritus from the stream. If this is the case, then only a small fraction of the hemlock needle input may ever reside in the stream long enough to become adequately conditioned to influence macroinvertebrate detritivore distribution and abundance in the substrate.

This experiment demonstrates that the source of detritus in the substrate can affect the distribution and abundance of macroinvertebrate detritivores. However, the quantitative response of macroinvertebrates to increases in the amounts of one detritus type could not be predicted. For example, in treatment HA with double the quantity of alder as in treatment LA, the biomasses of most chironimid taxa were increased over the values in treatment LA, but their densities were decreased. However, the densities and biomasses of the other taxa were decreased to levels below the ND treatment in treatments LA and/or HA. Thus, doubling the amount of alder detritus did not produce a correlated increase of macroinvertebrate biomass and density. Instead, macroinvertebrate detritivores responded to the increases in a species-specific manner. The complex response of macroinvertebrates to treatment HA may be related to subtle differences in other environmental factors that potentially occurred when alder quantity was increased. In particular, the higher

quantity of alder may have increased the biological oxygen demand, thereby affecting the colonization success of some taxa or the outcome of interactions between or among macroinvertebrate taxa.

Most of the macroinvertebrates that colonized the experimental treatments were either collector–gatherer or shredder detritivores (Appendix), but the response of a particular species to a detritus treatment could not be predicted from knowledge of the functional feeding guild membership of the species. Even in this experiment, where all other important variables such as substrate and current velocity were standardized, detritivore distribution and abundance was only partially explained by measured variations in the sources and quantity of the detritus food resource. Clearly then, the concept of functional feeding guilds is not useful for quantitatively predicting macroinvertebrate density or biomass at the microhabitat scale because macroinvertebrates are apparently responding to changes in detritus source and quantity in a species-specific manner rather than as a guild.

Culp et al. (1983) established that the microdistribution of many detritivorous taxa centered upon the presence or absence of detritus food particles, instead of particular substrate types. The present study further indicates the important influence that detritus source and quantity has on macroinvertebrate microdistribution. Although the particle sizes and quantities of detritus trapped within the streambed may be greatly influenced by substrate composition (Rabeni and Minshall 1977; Culp et al. 1983), our experiments underscore the accentuated importance of LPOM and MPOM detritus in the substrate as factors that strongly influence macroinvertebrate microdistribution at the species, rather than trophic feeding assemblage level.

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## References

ANDERSON, N. H., AND E. J. GRAFIUS. 1975. Utilization and processing of allochthonous material by stream Trichoptera. Verh. Int. Ver. Limnol. 19: 3022–3028.

ANDERSON, N. H., AND J. R. SEDELL. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annu. Rev. Entol. 24: 351–377.

CULP, J. M., S. J. WALDE, AND R. W. DAVIES. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. Can. J. Fish. Aquat. Sci. 40: 1568–1574.

CUMMINS, K. W. 1974. Structure and function of stream ecosystems. BioScience 24: 631–641.

CUMMINS, K. W., AND M. J. KLUG. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. 10: 147–172.

EGGLISHAW, H. J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. J. Anim. Ecol. 33: 463–476.

1969. The distribution of benthic invertebrates on substrata in fast-flowing streams. J. Anim. Ecol. 38: 19–33.

ELLIOTT, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. 25: 160 p.

FISHER, S.G., AND G. W. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 421–439.

HARGRAVE, B. H. 1969. Epibenthic algal production and community respiration in the sediments of Marion Lake. J. Fish. Res. Board Can. 26: 588–597.

IVERSON, T. M. 1973. Decomposition of autumn-shed beech leaves in a springbrook and its significance for the fauna. Arch. Hydrobiol. 72: 305–312.

JAKSIE, F. M. 1981. Abuse and misuse of the term "guild" in ecological studies. Oikos 37: 397–400.

KAUSHIK, N. K., AND H. B. N. HYNES. 1971. The fate of dead leaves that fall into streams. Arch. Hydrobiol. 68: 465–515.

KLINKA, K., F. C. NUSZDORFER, AND L. SKODA. 1979. Biogeoclimatic units of central and southern Vancouver Island. Province of British Columbia Ministry of Forests. 120 p.

MINSHALL, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology 48: 139–149.

MINSHALL, G. W., AND J. N. MINSHALL. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (USA) stream. Hydrobiologia 55: 231–249.

NEAVES, P. I. 1978. Litter fall, export, decomposition and retention in Carnation Creek, Vancouver Island. Fish. Mar. Serv. Tech. Rep. 809: 45 p.

PECKARSKY, B. L. 1980. Influence of detritus upon colonization of stream invertebrates. Can. J. Fish. Aquat. Sci. 37: 957–963.

PETERSON, R. C., AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream. Freshwater Biol. 4: 343–368.

RABENI, C. F., AND G. W. MINSHALL. 1977. Factors affecting microdistribution of stream benthic insects. Oikos 29: 33–43.

REICE, S. R. 1974. Enviromental patchiness and the breakdown of leaf litter in a woodland stream. Ecology 55: 1271–1282.

1978. The role of detritivore selectivity in species specific litter decomposition in a woodland stream. Vehr. Int. Ver. Limnol. 20: 1396–1400.

1980. The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream. Ecology 61: 580–590.

ROOT, R. B. 1967. The niche exploitation pattern of the blue-grey gnatcatcher. Ecol. Monogr. 37: 317–350.

SEDELL, J. R., F. J. TRISKA, J. D. HALL, N. H. ANDERSON, AND N. H. LYFORD. 1974. Sources and fates of organic inputs in coniferous forest streams, p. 57–69. *In* R. H. Waring and R. L. Edmonds [ed.] Integrated research in the coniferous forest biome. Conif. Biome, Ecosyst. Anal. Stud., US/IBP, Bull. No. 5. University of Washington, Seattle, WA.

SEDELL, J. R., F. J. TRISKA, AND N. S. TRISKA. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. I. Weight loss and associated invertebrates. Verh. Int. Ver. Limnol. 19: 1617–1627.

STOCKNER, J. G., AND K. R. S. SHORTREED. 1976. Autotrophic production in Carnation Creek, a coastal rainforest on Vancouver Island, British Columbia. J. Fish. Res. Board Can. 33: 1553–1563.

STRAHLER, A. N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union 38: 913–920.

VOLLENWEIDER, R. A. [ED.] 1969. A manual on methods for measuring primary production in aquatic environments. IBP Handbook No. 12. Blackwell Scientific Publications, Oxford. 213 p.

WARD, G. M., AND K. W. CUMMINS. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albumanus* (Meigen) (Diptera: Chironomidae). Ecology 60: 57–64.

WRONA, F. J., J. M. CULP, AND R. W. DAVIES. 1982. Macroinvertebrate subsampling: a simplified apparatus and approach. Can. J. Fish. Aquat. Sci. 39: 1051–1054.

ZAR, J. H. 1974. Biostatistical analyses. Prentice-Hall Inc., Englewood Cliffs, NJ. 620 p.

APPENDIX. Densities (thousands/$m^2$) and biomasses ($g/m^2$) of the 12 taxa with significant differences among the no detritus (ND), low hemlock (LH), low alder (LA), and high alder (HA) treatments. Functional feeding guild classification: (C = collector; G = gatherer; Sc = scraper; Sh = shredder; E = engulfers.

| Taxa | ND | | LH | | LA | | HA | | Guild |
|---|---|---|---|---|---|---|---|---|---|
| | Density | Biomass | Density | Biomass | Density | Biomass | Density | Biomass | |
| Ephemeroptera | | | | | | | | | |
| *Baetis hageni* Eaton | 1.42 | 0.09 | 1.01 | 0.06 | 1.44 | 0.14 | 0.61 | 0.04 | CG |
| *Cinygmula ramaleyi* (Dodds) | 0.71 | 0.46 | 0.32 | 0.23 | 1.44 | 0.69 | 0.27 | 0.19 | CSc |
| Chironomidae | | | | | | | | | |
| *Brillia* Kieff. | 0.19 | 0.01 | 0.03 | 0.01 | 3.89 | 0.32 | 3.60 | 0.46 | Sh |
| Chironomidae pupae | 0.43 | 0.03 | 0.24 | 0.01 | 1.12 | 0.16 | 0.80 | 0.12 | — |
| *Micropsectra* Kieff. | 0.40 | 0.01 | 1.49 | 0.01 | 2.93 | 0.04 | 3.79 | 0.05 | CG |
| *Thienemannimyia* group (Fittk.) | 4.61 | 0.04 | 4.00 | 0.02 | 8.91 | 0.04 | 5.17 | 0.04 | E |
| *Parametriocnemus* (Geotgh.) | 0.0 | 0.0 | 0.0 | 0.0 | 0.59 | 0.01 | 0.48 | 0.01 | CG |
| *Polypedilum* (*Polypedilum*) Kieff. | 1.60 | 0.04 | 3.47 | 0.03 | 10.51 | 0.28 | 6.00 | 0.25 | Sh |
| *Orthocladius* (v.d. Wulp.) | 1.45 | 0.01 | 1.12 | 0.01 | 3.63 | 0.01 | 0.40 | 0.01 | CG |
| *Corynoneura* (Winn.) | 9.15 | 0.03 | 7.41 | 0.02 | 6.13 | 0.01 | 3.81 | 0.01 | CG |
| *Synorthocladius* Thien. | 1.09 | 0.01 | 0.85 | 0.01 | 0.80 | 0.01 | 0.05 | 0.01 | CG |
| *Thienemanniella* Kieff. | 10.35 | 0.03 | 9.33 | 0.02 | 5.28 | 0.02 | 3.09 | 0.02 | CG |

# Bias in the Estimation of Functional Relationships from Time Series Data

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Functional relationships, such as stock–recruitment curves, are generally estimated from time series data where natural "random" factors have generated both deviations from the relationship and also informative variation in the independent variables. Even in the absence of measurement errors, such natural experiments can lead to severely biased parameter estimates. For stock–recruitment models, the bias is misleading for management: the stock will appear too productive when it is low, and too unproductive when it is large. The likely magnitude of such biases can and should be determined for any particular case by Monte Carlo simulations.

Les relations fonctionnelles, comme celles des courbes stock–recrutement, sont généralement estimées à partir de données de séries chronologiques où des facteurs naturels « aléatoires » ont provoqué une distorsion de la relation et une variation informative des variables indépendantes. Même en l'absence d'erreurs de mesures, ces expériences naturelles peuvent être source d'une distorsion importante des estimations de paramètres. Dans le cas des modèles stock–recrutement, le biais est source d'erreur de gestion : le stock apparaît trop productif quand il est peu important et trop peu productif quand il est important. L'importance probable de ce genre biais peut et doit être déterminée dans chaque cas par simulations de Monte-Carlo.

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Relationships between stock size and processes such as recruitment and growth are of fundamental importance in fisheries stock assessment, since these relationships define the best stock level for sustained production. Inferences about the relationships can seldom be based on deliberate, controlled experiments where the stock is held at various levels while the responses are measured. Instead, we count on natural variation in the processes themselves, particularly in recruitment rates, to provide some of the necessary variation. This reliance on natural "experiments" could become more important in the future, as management agencies become more adept at regulating exploitation rates and are pressed to do so as a means to provide economic stability.

Functional relationships are usually estimated by treating stock sizes (and other causal variables) as though they had been chosen experimentally, and then applying standard statistical recipes for regression analysis to the data. This approach can fail badly, however, when there are large measurement errors in the independent variables such as escapement levels (Ludwig and Walters 1981; Walters and Ludwig 1981) and/or autocorrelations among deviations (Box and Jenkins 1976). My objective here is to point out a third and equally serious source of bias when standard recipes are used; the bias is caused by correlation between deviations and subsequent levels of the independent variables when these levels are not chosen through deliberate experimental design.

## How the Bias Arises

To simplify the following discussions, I will consider only situations where the functional relationship of concern can be transformed to the linear-in-parameters form

$$(1) \quad y = X\beta + W$$

where $y$ is a time-ordered vector of dependent variable values, such as recruitment rates in a sequence of years, $X$ is a design matrix whose columns consist of known functions of independent variables, such as stock sizes also ordered over time, $\beta$ is a vector of unknown "production parameters" to be estimated, and $W$ is a vector of random, uncorrelated "environmental effects" due to factors not considered in $X$. The particular concern here is with situations where the elements $W_t$ may be large, and where their influence on $y_t$ is transmitted (through the natural system dynamics) into effects on the rows of $X$ at times $t + 1$, $t + 2$, etc. A good example of equation (1) occurs in stock–recruitment assessment with the stochastic Ricker model $R_t = S_{t-1}\, e^{a - bS_{t-1} + W_t}$ where $R_t$ = recruits and $S_t$ = spawners. In this case, it is usual to take

$$y_t = \log (R_t/S_{t-1}),\ \beta = \begin{pmatrix} a \\ b \end{pmatrix},\ W_t$$

as defined, and

$$X = \begin{bmatrix} 1 - S_0 \\ 1 - S_1 \\ \cdot \quad \cdot \\ \cdot \quad \cdot \\ \cdot \quad \cdot \\ 1 - S_{t-1} \end{bmatrix}.$$

Notice that $W_t$ affects $R_t$, which will in turn affect $S_t$, $R_{t+1}$, etc., unless the escapement $S_t$ is deliberately chosen to be independent of $R_t$ (i.e. by deliberately *not* allowing more spawners in years of high recruitment). The results I now present will apply equally well to messier cases involving nonlinear estimation.

The standard recipe for estimating $\beta$ in equation (1) is the least squares result

$$(2) \quad \hat{\beta} = (X'X)^{-1}X'y.$$

For designed experiments the $\hat{\beta}$ are unbiased and are maximum likelihood when the $W_t$ are normally distributed with equal variance $\sigma_w^2$. Now, suppose we substitute equation (1) into (2) and simplify a little; the result is

$$(3) \quad \hat{\beta} = \beta + (X'X)^{-1}X'W.$$

Here, $(X'X)^{-1}X'W$ is the vector of errors in the parameter estimates, and its elements should all have expected value zero (across realizations of the random vector $W$) if the estimates are to be unbiased. This condition is obviously satisfied for designed experiments where $X$ is chosen in advance, independently of $W$.

For "natural experiments" where $W$ is allowed to influence the $X$ matrix elements, the error term $(X'X)^{-1}X'W$ becomes a complicated function of the system dynamics. There is no reason at all to hope that it will have a zero expected value (i.e. no bias) with respect to $W$, especially for small sample sizes as are common in stock recruitment analysis. Consider for example the Ricker model mentioned; in this case, the equation (3) element for $b$ can be written simply as

$$(4) \quad \hat{b} = b + \frac{1}{SS_x}\left[\frac{\left(\sum_{t=1}^{T} S_{t-1}\right)\left(\sum_{t=1}^{T} W_t\right)}{T} - \sum_{t=1}^{T} S_{t-1}W_t\right]$$

where $SS_x$ is the usual sum of squares

$$\sum_{t=1}^{T} (S_{t-1} - \bar{S})^2$$

that measures contrast in the independent variable values. In equation (4), the term $\Sigma S_{t-1}W_t$ causes no problem, since $S_{t-1}$ and $W_t$ are independent by assumption. However, consider the term $(\Sigma S)(\Sigma W)/T$. Though this term vanishes as the sample size $T$ becomes very large, for realistic situations it contains many product terms like $W_tS_t$, $W_tS_{t+1}$, and $W_tS_{t+2}$. These terms, which represent correlation or covariance between disturbances and future states, do not have zero expected values (i.e. are not independent) for natural experiments. Even if the effect of $W_t$ on future states damps off quickly over time, so only the $W_tS_t$ correlations are significant, $\hat{b}$ will have a significant positive bias that (i) is a complex function of $a$ and $b$ and (ii) increases with the disturbance variance $\sigma_w^2$. Thus the best conditions for observing natural variation (high $\sigma_w^2$) are also the worst for bias. To further complicate assessment of the bias, increasing $\sigma_w^2$ leads to reduced covariance between $W_t$ and longer term states $S_{t+1}$, $S_{t+2}$, etc.

Another way to think about the Ricker example is to recognize that there are two relations between escapement and recruitment:

$$R_t = S_{t-1}\, e^{a - bS_{t-1} + W_t}$$

and

$$S_t = s_t R_t$$

where $s_t$ is the proportion of recruits $R_t$ that survive to spawn in year $t$ ($s_t$ is a "control variable" for management). Combining these two relations, the model can be written as

$$R_{t+1} = s_t R_t\, e^{a - bs_t R_t + W_t}$$

which is a nonlinear autoregression model for $R_t$ even if $s_t$ is held constant. Standard regression estimates for $a$ and $b$ would be biased even if this autoregression were linear (e.g. $R_{t+1} = a + bR_t + W_t$; see Box and Jenkins 1976, Chap. 7).

## Magnitude of the Bias in a Stock–Recruitment Example

For the Ricker model, both $\hat{a}$ and $\hat{b}$ are biased upward in situations where the exploitation rate $(R_t - S_t)/R_t$ or $1 - s_t$ has been relatively constant at a moderate level so that there have been no strong trends in $S_t$ over time ($SS_x$ in equation (4) mostly due to $W_t$ effects). Such situations are common for Pacific salmon (Walters et al. 1982). Upward bias in $\hat{a}$ results in an overestimate of the optimum exploitation rate, and upward bias in both parameters results in an underestimate of the optimum spawning stock (to maximumize average catch).

To estimate the likely magnitude of this bias, I generated 1000 fake data sets each with 10 stock–recruit data pairs. The Ricker model was used to generate each data set (Monte Carlo trial), with parameter values $a = 1.0$ (typical for British Columbia pink (*Oncorhynchus gorbuscha*) or chum (*Oncorhynchus keta*) salmon), $b$ ranging from 0.3 to 1.0, and $\sigma_w$ ranging from 0.0 to 1.0. For each case the initial stock size $S_0$ was set to 1.0, and the harvest rate was held constant over time at 0.5. This harvest policy tended to hold the spawning stocks steady at levels around $1/2b$, except for random fluctuations due to effects of $W_t$ on $R_t$. For each case, I estimated the (known) $a$ and $b$ parameters by standard linear regression.

The resulting bias estimates (average estimation error across many cases) were almost independent of the choice of $b$ parameter, but increased strongly for values of $\sigma_w$ above 0.1. For values of $\sigma_w$ that are realistic for Pacific salmon (0.5–1.0), the $a$ parameter was overestimated by an average of 30%, and the $b$ parameter was underestimated by a similar amount. For each case, I also calculated estimated and "actual" optimum exploitation rates and escapements for maximizing average yield; these were overestimated and underestimated, respectively, by 30 and 50% for realistic values of $\sigma_w$.

Why has the bias implied by equation (3) not previously been stressed by fisheries analysts? I originally noticed it quite by accident, while doing Monte Carlo simulations to determine effects of harvest policies on estimation precision. I searched in vain for reference to the problem in various statistics texts; one reason for the oversight became obvious. Functional relationships and associated dynamic behavior are usually viewed as deterministic curves that are observed with random measurement error; future states (independent variables) are usually

ignored. Also, the problem is analytically subtle, as evidenced by equation (4); this equation can be rewritten as

$$(5)\quad \hat{b} = b - \frac{\sum_{t=1}^{T} (S_{t-1} - \bar{S})(W_t - \bar{W})}{SS_x}.$$

In this form it appears intuitively that the error term should have expectation zero, since the cross-product terms $(S_{t-1} - \bar{S})(W_t - \bar{W})$ involve only independent variables $(S_{t-1}, W_t)$ if $\bar{S}$ and $\bar{W}$ are fixed (the problem is that they are not fixed).

## Options for Improved Estimation

There are at least three possible ways to deal with the bias implied by equation (3). First, in principle it is possible to avoid it by developing a complete model for the stochastic process leading to the observations $[X, y]$ as a function of $\beta$. This model would constitute a likelihood function for $[X, y]$ given $\beta$, thus permitting full application of likelihood and Bayesian estimation procedures. Unfortunately, such models are usually complicated from a computational viewpoint, and may not provide less biased estimators in the end.

Second, approximate bias correction formulae can be developed for specific cases. For example, equations (4) and (5) lead to a bias correction term involving a weighted sum of correlations between $W_{t-k}$ and $S_t$ for various lags $k$; the initial (biased) estimates $\hat{a}$ and $\hat{b}$ are used to estimate the $W_t$ and hence the $W$–$S$ correlations. Such approximations are tedious to derive, depend on the bias being only weakly dependent on the unknown parameter $\beta$, and require extensive Monte Carlo testing to establish their reliability.

Third, one can conduct Monte Carlo simulations to estimate the bias numerically for a range of parameter combinations around the nominal estimates obtained by standard procedures. The idea is simply to generate a large number of fake data sets for which the correct parameter values are known, and then give these data sets to the estimation procedure and record its performance. Beyond measuring bias, an advantage of this approach is that the fake data sets can always be made more "realistic" than assumed by the estimation procedure (by generating them with more complex models), and hence other measures of the robustness of the procedure can be obtained. Monte Carlo methods do not guarantee discovery of important weaknesses in estimation procedures, since the researcher may fail to identify and test some critical assumption, but they at least offer a step forward from acceptance of procedures on faith.

## References


BOX, D. E. P., AND G. M. JENKINS. 1976. Time series analysis: forecasting and control. Holden-Day, San Francisco, CA. 575 p. (See p. 208–284)

LUDWIG, D. AND C. J. WALTERS. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. Can. J. Fish. Aquat. Sci. 38: 711–720.

WALTERS, C. J., R. HILBORN, M. STALEY, AND F. WONG. 1982. Status and potential yields of fish stocks on Pacific coast of Canada. Report to the Pearse Commission on Pacific fisheries policy. 133 p. (Available from ESSA Ltd., 678 W. Broadway, Vancouver, B.C. V5Z 1G6)

WALTERS, C. J., AND D. LUDWIG. 1981. Effects of measurement errors on the assessment of stock–recruitment relationships. Can. J. Fish. Aquat. Sci. 38: 704–710.

# Search and Stock Depletion: Theory and Applications

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A general theory for the estimation of stock size from search data is developed. In the theory, it is assumed that discrete aggregations (schools of fish, beds of clams) are encountered. The search model is an extension of the Poisson process to include depletion. The theory provides a way of estimating stock size and confidence intervals around the estimate, as well as the ability to predict future catches for a given level of effort. Three applications of theory are described: (1) estimating stock size when there is no catch; (2) determining, in real time, the length of fishing seasons; and (3) an empirical study of stock assessment of Pacific ocean perch (*Sebastes alutus*) near Rennell Sound, British Columbia.

Nous avons mis au point une théorie générale sur l'estimation des stocks d'après des données de recherche. Cette théorie suppose qu'on rencontre des groupes séparés (bancs de poissons, colonies de clams). Nous avons élargi le procédé de Poisson pour tenir compte de l'amenuisement. La théorie permet d'estimer l'importance des stocks, l'intervalle de confiance de l'estimation et la possibilité de prévoir les prises en fonction d'un effort de pêche donné. Nous décrivons trois applications : (1) estimation des stocks lorsqu'il n'y a pas de prises ; (2) détermination, en temps réel, de la longueur de la saison de pêche ; et (3) étude empirique de l'évaluation des stocks de sébastes (*Sebastes alutus*) près de la baie Rennell en Colombie-Britannique.

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## 1. Introduction

One of the thorniest problems in the management of fisheries is the problem of determining stock abundance. For this reason, biomass surveys are often run by the managing organizations. In some fisheries, the cost of the survey is about the same as the economic value of the fishery (C. Clark, Mathematics Department, University of British Columbia, Vancouver, B.C., pers. comm.).

In those cases without a stock survey, some other procedure for estimating stock size is needed. Perhaps the most common is the model assuming a linear relationship between catch and population:

$$H = qEP$$

where $H$ is harvest, $E$ is fishing effort, $P$ is population size, and $q$ is a proportionality coefficient (the catchability coefficient). With this model $H/E$, catch per unit effort (CPUE) is proportional to population. To use this model, one needs some measure of fishing effort, a quantity that is notoriously hard to measure in any real fishery (e.g. see Rothschild 1972; Wilen 1979). Even if effort could be measured accurately, the CPUE model does not always produce measures of population size that reflect the population (e.g. see Clark and Mangel 1979).

One case in which CPUE is expected to break down is when the fishermen spend considerable amounts of time searching for dense schools or aggregates of fish (this is actually the case considered by Clark and Mangel 1979 for tuna). In this case, the search effort is as important to the estimate of population size as is the time spent harvesting, so that one should consider the relationship between search effort and stock size (Mangel 1982). There is a growing body of literature on the role of search in fisheries (e.g. see Allen and Punsly 1984; Butterworth 1982; Cooke 1984; Neyman 1949; Paloheimo 1971; Rothschild 1977). Allen and Punsly (1984), in particular, advocated the concept of using catch per hour searching as a way of estimating abundance. They used a very simple search model, followed by regression techniques.

In this paper, we introduce a new theory for the estimation of stock size using search data. The model and development of the theory are presented in section 2. Sections 3, 4, and 5 are management oriented. Section 3 considers the problem of estimating the stock size when there is no catch. In section 4, we show how search theory can be used to provide real time determination of the length of fishing seasons. Section 5 contains the results of an empirical study on Pacific ocean perch (*Sebastes alutus*) off Rennell Sound, British Columbia, for the estimation of stock size and prediction of harvest as a function of effort. Throughout the paper, we are concerned with search and stock depletion in a single fishing season, so we ignore recruitment. The theory that we develop, however, can be extended to include recruitment. Section 6 contains comments

on implementation of this work, as well as a discussion of some of the extensions currently under investigation.

The innovative aspects of the work presented in this paper include the following:

(1) A general theory that relates stock abundance to search rates and includes depletion of the stock due to harvesting (cf. Allen and Punsly 1984 where depletion is ignored). This theory involves two parameters: stock size, $N$, and a measure of search effectiveness, $\epsilon$.

(2) An operational definition of $\epsilon$ that is independent of any data set that one would analyze. The parameter $\epsilon$ is related to operational variables such as vessel speed, detection width, and size of the region being searched.

(3) A combination of Bayesian and maximum likelihood methods for estimating the parameter $N$. In particular, maximum likelihood methods are used to provide an estimate of $N$, $\hat{N}$, and Bayesian confidence intervals are then derived. The Bayesian methods are particularly useful when there is a lack of data; e.g. how does one estimate stock abundance in the absence of catch.

## 2. Search Model and Theory

Perhaps the simplest search model is the Poisson process. In this model, one assumes that the search process is random and that

$$\begin{aligned} &\text{Prob}\{\text{find another school in the next } \Delta t\} = \lambda \Delta t \\ &\text{Prob}\{\text{do not find another school in the next } \Delta t\} = 1 - \lambda \Delta t \\ &\text{Prob}\{\text{anything else}\} = 0 \end{aligned} \tag{2.1}$$

where $\Delta t$ is a small time interval and $\lambda$ is a parameter. If the search is random and only one school is present, $\lambda$ can be estimated using classical search theory (Koopman 1980), which gives

$$\lambda = \frac{Wv}{A} \tag{2.2}$$

where $W$ is the sweep width of the searcher (for purposes of fisheries, $W$ can be thought of as the area of the net opening or, the detection width of the echosounder), $v$ is the speed of the searcher, and $A$ is the area (or volume) of water where the school might be.

It is worthwhile to examine in detail the assumptions that lead to (2.1). The most important of these are (i) cohesive and identifiable schools, (ii) random search, and (iii) no depletion of the stock. Certainly, not all types of fish move in cohesive and identifiable schools but there are a sufficient number of species that do (tuna, some groundfish, whales) to make a theory concerned with the search for schools sufficiently interesting. It is not crucial that the fish spend all of the time in schools, only that the search is for schools. It is also true that fishermen probably do not execute random searches. This, however, does not mean that the ultimate search process cannot be modeled as random. First, the schools being sought may move randomly or quasi-randomly. Second, on the small scale of tracklines, ostensibly nonrandom searches take on considerable fluctuations (Koopman 1980). Third, there are experiments to indicate the generality of exponential models for times between detections (equivalent to a random search). These experiments (Washburn 1981, p. 2–8) involved a computer joystick game in which an intelligent pursuer sought an intelligent evader. The experiments indicate that a random search model provides an excellent description of the overall detection process. Fourth, if there is considerable set time after a discovery, the information gained in locating a school may be dissipated so that the search for the next school is random. Allen and Punsly (1984) examined the hypothesis of random search and concluded that it is acceptable. They also pointed out that data often exhibit "overdispersion," i.e. too may intervals between detections that are too long or too short. Mangel and Clark (1983) showed that such deviations from pure negative exponential distributions can arise in the following way. Assume that locally, search is random with parameter $\lambda$, but that $\lambda$ has a distribution. For example, if one examines $1^0 \times 1^0$ cells, then in each cell it could be assumed that, conditioned on $\lambda$, the number of schools found in $(0, t)$ is Poisson with parameter $\lambda t$. If $\lambda$ has a distribution, say a gamma distribution, then the unconditional distribution of catch is negative binomial, which exhibits overdispersion, relative to the Poisson distribution. The underlying search mechanism, however, is still random. The assumption of random search will be used in this paper. The third assumption leading to (2.1) is the lack of depletion. This makes no sense if one is trying to estimate the effects of harvesting on stock abundance. In particular, if depletion is not taken into account, there is a tendency to considerably overestimate abundance.

In this paper, a methodology is introduced under the following assumptions:

(i) The search process involves the search for discrete and identifiable schools. (This does not imply, however, that the fish being sought always school — only during the search process. An example is given in section 5.)

(ii) The times between detections are independent, exponential random variables (thus corresponding to random search); the distribution of these variables changes due to search.

(iii) When a detection occurs, the entire school is fished out. The parameter characterizing the search rate is then decremented.

Further discussion, and ways to modify these assumptions, is found in section 6. Although it may appear that these assumptions are too restrictive to provide any useful results, this is not the case as the work (including an empirical study) reported in sections 3–5 demonstrates. Clearly, one would like a more general theory, but there must always be a starting point.

To modify (2.1) to include depletion, we keep the assumption of random search but now assume that many schools (or aggregations) are present and that detections of different schools are independent events. With these assumptions, a reasonable modification of (2.1) is as follows:

$$\begin{aligned} &\text{Prob}\{\text{find another school in the next } \Delta t | i \text{ were found thus far}\} = (\lambda - i\epsilon)\Delta t \\ &\text{Prob}\{\text{do not find another school in the next } \Delta t | i \text{ were found thus for}\} = 1 - (\lambda - i\epsilon)\Delta t. \end{aligned} \tag{2.3}$$

There are two parameters in this model: $\lambda$ and $\epsilon$. Since $\lambda$ is proportional to the initial rate of detections, it is really unknown. The situation is better with $\epsilon$, however. Suppose that there were exactly $n$ schools present initially. Then the independence assumption leads to

$$\lambda = n \frac{Wv}{A}.$$

After the first detection, there are $n - 1$ schools present, so $\lambda$

would be replaced by $(n-1)Wv/A$. Consequently

$$\epsilon = \frac{Wv}{A}. \tag{2.4}$$

The first contribution of search theory is to provide this expression for $\epsilon$ in terms of operational variables (cf. Goudie and Goldie 1981). Note that $\epsilon$ is a measure of search ability. An example of the calculation of the sweep width $W$ is given in section 5. Observe too that $\epsilon$, as defined by (2.4), can be computed outside of the data being analyzed.

When $k$ searchers are present and search independently, (2.3) is modified by replacing $(\lambda - i\epsilon)$ by $k(\lambda - i\epsilon)$. With these assumptions, one finds that the number of schools discovered has a binomial distribution with parameters $N = \lambda/\epsilon$ and $p = 1 - e^{-k\epsilon t}$. Thus

$$\begin{aligned} &\Pr\{k \text{ searchers discover } n \text{ schools in } (0, t)\} \\ &\quad \equiv p(k, n, t, \epsilon) \\ &\quad = \binom{\lambda/\epsilon}{n}(1 - e^{-k\epsilon t})^n (e^{-k\epsilon t})^{(\lambda/\epsilon - n)}, \quad n = 0, 1, \ldots, \lambda/\epsilon \\ &\quad = 0 \qquad \text{otherwise.} \end{aligned} \tag{2.5}$$

Equation (2.5) is derived by standard probabilistic methods (e.g. Feller 1968). According to (2.5), the expected number of schools discovered, $E_t(n)$, and variance in the number of schools discovered, $V_t(n)$, in the interval $(0, t)$ are

$$\begin{aligned} E_t(n) &= \frac{\lambda}{\epsilon}(1 - e^{-k\epsilon t}) \\ V_t(n) &= \frac{\lambda}{\epsilon}(1 - e^{-k\epsilon t})e^{-k\epsilon t}. \end{aligned} \tag{2.6}$$

Note that $\lambda/\epsilon$ can be interpreted as the initial number of schools. Equations (2.5) and (2.6) refer to the search time only. If each aggregation requires a harvest time $\tau_h$, the total time spent fishing and searching is $T = t + n\tau_h$. Since $n$ is a random variable, then so is $T$, and its distribution function is easily found from (2.5). In most cases, however, the inverse problem is of more interest, i.e. given $T$ find the estimates of $t$ and $n$. This problem is discussed in section 5.

Equations similar to (2.5) and (2.6) were derived by DeLury ((1947, 1951); Seber (1982, p. 296)) in his classic work on stock estimation. The difference is that in the current model, $\epsilon$ is given in terms of operational parameters (area searched, vessel speed, and sweep width) and can thus be determined independently of the data being analyzed. Without the operational interpretation of $\epsilon$, the estimation problems become much more difficult. For example, the methods of Leslie and DeLury (see Seber 1982, p. 296, for a good discussion) involve regressions that seek to determine both the initial size of the population and the catchability coefficient, which is analogous to $\epsilon$. These methods can lead to negative estimates of stock abundance, something that never happens with the methods advocated in this paper. Thus, there is considerable gain made by using an operational definition of $\epsilon$ that is independent of the actual fishing process.

In general, $\lambda$ (or $\lambda/\epsilon$) will be unknown. Two different methods for estimating $\lambda$, when $\epsilon$ is known, are given below. One method fixes the number of schools detected in a variable time. The other method fixes the time interval and allows the number of schools detected to vary. For simplicity, assume that there is only one searcher, so that $k = 1$. Suppose that this searcher discovers $n$ schools and that $T_i$, $i = 1, \ldots, n$ was the observed time between the $(i-1)$st and $i$th detections. The total search time $T$ is

$$\sum_{i=1}^{n} T_i.$$

According to the search model (2.3), the random variable $\tilde{T}_i$, which is the time between the $(i-1)$st and $i$th detections, is exponentially distributed with parameter $\lambda - (i-1)\epsilon$. The $\tilde{T}_i$, $i = 1, \ldots, n$ are independent but not identically distributed random variables. The likelihood, $\mathcal{L}$, of the set $\{T_1, \ldots, T_n\}$ is then

$$\mathcal{L} = \prod_{i=1}^{n} (\lambda - (i-1)\epsilon)e^{-(\lambda-(i-1)\epsilon)T_i}. \tag{2.7}$$

The maximum likelihood estimator (MLE) for $\lambda$ is derived from (2.7). Taking the derivative of the logarithm of $\mathcal{L}$ gives

$$\frac{\partial}{\partial\lambda}\log\mathcal{L} = \sum_{i=1}^{n}\left\{\frac{1}{\lambda - (i-1)\epsilon} - T_i\right\}. \tag{2.8}$$

Setting the right hand side of (2.8) equal to zero gives the $n$th-order algebraic equation

$$\sum_{i=1}^{n}\frac{1}{(\lambda - (i-1)\epsilon)} = \sum_{i=1}^{n} T_i = T. \tag{2.9}$$

(Note that setting $\epsilon = 0$ gives $\lambda = n/T$, the MLE for a Poisson process.)

The second derivative of $\log\mathcal{L}$ is given by

$$\frac{\partial^2}{\partial\lambda^2}\log\mathcal{L} = -\sum_{i=1}^{n-1}\frac{1}{(\lambda - (i-1)\epsilon)^2}. \tag{2.10}$$

Since the second derivative is negative, the solution of (2.9) is indeed a MLE.

When $\epsilon$ is small, the solution of equation (2.9) can be found approximately as a power series in $\epsilon$. This approach gives

$$\lambda = \frac{n}{T} + \left(\frac{n-1}{2}\right)\epsilon - \frac{(n^2-1)T}{12n}\epsilon^2 + 0(\epsilon^3). \tag{2.11}$$

To employ the second estimate for $\lambda$, fix $t$ and set $N = \lambda/\epsilon$. In light of equation (2.5), $N$ is the initial number of schools. Equation (2.5) is then a likelihood equation for $N$, given that $n$ schools were discovered. In what follows, we set $k = 1$. Results for $k > 1$ are obtained by replacing $t$ by $kt$. Thus, the likelihood is

$$\begin{aligned} L(N; n) &= \binom{N}{n}(1 - e^{-\epsilon t})^n e^{-\epsilon t(N-n)}, \quad N = n, n+1, \ldots \\ &= 0 \qquad \text{otherwise.} \end{aligned} \tag{2.12}$$

The problem is now that of estimating $N$ in the binomial distribution on the basis of a single observation on $n$. Somewhat tongue-in-cheek, this problem is aptly described as "capture – recapture – without recapture." (Other problems in which the binomial parameter $N$ must be estimated are discussed by Blumenthal and Dahiya (1981) and Olkin et al. (1981).)

First consider the MLE for $N$. It is most easily found through the likelihood ratio

$$\frac{L(N+1; n)}{L(N; n)} = \frac{\binom{N+1}{n}}{\binom{N}{n}}e^{-\epsilon t} = \left\{\frac{N+1}{N+1-n}\right\}e^{-\epsilon t}. \tag{2.13}$$

The ratio in (2.13) is 1 if

$$(2.14)\quad \left(\frac{N+1}{N+1-n}\right) e^{-\epsilon t} = 1.$$

Solving for $N$ gives

$$(2.15)\quad N = \frac{n}{1-e^{-\epsilon t}} - 1.$$

From (2.15) it follows immediately that the MLE for $N$ is

$$(2.16)\quad \hat{N} = \left[\frac{n}{1-e^{-\epsilon t}}\right].$$

Here, $[x]$ is the integer part of $x$. From (2.16), it follows that the estimate for $\lambda$ is $\lambda_2 = N\epsilon$. The two estimates (based on (2.9) and (2.16)) are identical to within order $\epsilon$ (Table 1).

Equation (2.16) is similar to the more common estimate, which reads

$$\text{Biomass} = \frac{\text{Catch}}{1-\exp\{-q\cdot\text{effort}\}}$$

where $q$ is the catchability coefficient and effort is measured in some aggregate form. The main differences are that in (2.16) $\epsilon$ is a completely operational variable and $t$ is search time only. In this sense, (2.16) is much less aggregated than the standard catch equation.

One could, in principle, try to "operationalize" $q$ by defining it in terms of operational parameters (e.g. Rothschild 1972, 1977). There is still the problem of the aggregation and definition of effort, however. The use of equation (2.16) avoids this problem.

Note that $\hat{N}$ depends upon both the catch and the elapsed search time $t$. From (2.16), one sees that $\hat{N}$ tends to increase with $n$, if $t$ is fixed. If no aggregates are encountered for a long time, $\hat{N}$ will eventually equal $n$. This indicates that the entire population was caught.

If a Bayesian view is adopted, the posterior distribution of $N$ (and thus of $\lambda$) can be calculated if a prior distribution $g(N)$ and an observation $n$ are given. If $g(N|n)$ denotes the posterior, then

$$(2.17)\quad g(N|n) = \frac{L(N;n)g(N)}{\sum_{N=n}^{\infty} L(N;n)g(N)}$$

where $L(N;n)$ is given by (2.12).

One choice for the prior distribution is the improper prior

$$(2.18)\quad g(N) \equiv \begin{cases} 1 & N = 0, 1, 2, \ldots \\ 0 & \text{otherwise.} \end{cases}$$

The prior distribution defined in (2.18) is improper because its sum is infinite. The posterior distribution, however, is a true probability distribution as the following calculation shows. For the improper prior (2.18), equation (2.17) becomes

$$(2.19)\quad g(N|n) = \frac{L(N;n)}{\sum_{N=n}^{\infty} L(N;n)},\quad N = n, n+1, \ldots$$

The identity

$$\sum_{N=n}^{\infty} \binom{N}{n} x^{N-n} = (1-x)^{-n-1}$$

TABLE 1. Comparison of estimates of $\lambda$ based on fixed $n$ ($\hat{\lambda}_1$) and fixed $t$ ($\hat{\lambda}_2$). Search time = 100 h; $k$ = 1 vessel.

| | | Schools found | | | |
|---|---|---|---|---|---|
| $n$ | $\epsilon$ | $\lambda_1$ | $n_{R1}$[a] | $\lambda_2$ | $n_{R2}$[a] |
| 10 | 0.01 | 0.153 | 5.31 | 0.150 | 5 |
| 15 | 0.01 | 0.232 | 8.22 | 0.230 | 8 |
| 20 | 0.01 | 0.313 | 11.1 | 0.310 | 11 |
| 25 | 0.01 | 0.390 | 14.0 | 0.390 | 14 |
| 30 | 0.01 | 0.470 | 17.0 | 0.470 | 7 |
| 10 | 0.005 | 0.124 | 14.9 | 0.125 | 15 |
| 15 | 0.005 | 0.188 | 22.6 | 0.190 | 23 |
| 20 | 0.005 | 0.252 | 30.3 | 0.250 | 30 |
| 25 | 0.005 | 0.315 | 38.1 | 0.315 | 38 |
| 30 | 0.005 | 0.379 | 45.7 | 0.379 | 46 |

[a] $n_{Ri}$ is the expected number of schools remaining, using estimator $\lambda_i$.

allows one to write the denominator in (2.19) as

$$(2.20)\quad \sum_{N=n}^{\infty} L(N;n) = \sum_{N=n}^{\infty} \binom{N}{n} (1-e^{-\epsilon t})^n e^{-\epsilon t(N-n)}$$
$$= (1-e^{-\epsilon t})^n (1-e^{-\epsilon t})^{-n-1}$$
$$= (1-e^{-\epsilon t})^{-1}.$$

Consequently, the posterior $g(N|n)$ becomes

$$(2.21)\quad g(N|n) = \binom{N}{n} (1-e^{-\epsilon t})^{n+1} e^{-\epsilon t(N-n)},$$
$$N = n, n+1, \ldots$$

A second choice is the noninformative prior (Martz and Waller 1982)

$$(2.22)\quad g(N) = \left(\frac{-\partial^2 L(N;n)}{\partial N^2}\right)^{1/2} \Bigg|_{\frac{\partial L(N;n)}{\partial N} = 0}.$$

A prior is called noninformative if the data only change the location, but not the shape, of the likelihood curve (Box and Tiao 1973, p. 32). The prior in (2.22) can not be computed analytically; but it is easy to find its value numerically. When calculating $g(N)$ in (2.22), the observation $n$ is eliminated by setting $\partial L(N;n)/\partial N = 0$ and solving for $n$ in terms of $N$.

Figures 1A and 1B show the posterior distribution on $N$ using (2.18) and (2.22). Since the results are so similar, the uniform prior will be used. If one sets $p = 1 - e^{-\epsilon t}$ and $q = e^{-\epsilon t}$, then (2.21) becomes

$$(2.23)\quad g(N|n) = \binom{N}{n} p^{n+1} q^{N-n},\quad N = n, n+1, \ldots$$
$$= 0 \qquad \text{otherwise.}$$

This form of (2.21) will be very useful in the sequel. Equation (2.23) can be used to construct Bayesian confidence intervals for $N$ around $\hat{N}$ by solving for the smallest $J^*$ such that

$$(2.24)\quad g(\hat{N}|n) + \sum_{j=1}^{J^*} [g(\hat{N}-j|n) + g(\hat{N}+j|n)] \geq \gamma$$

where $\gamma$ is the desired confidence level. Equation (2.24) is easily evaluated on a desk-top microcomputer once a prior $g(N)$ is given. Table 2 provides an example of such a confidence interval, for the improper prior (2.18).

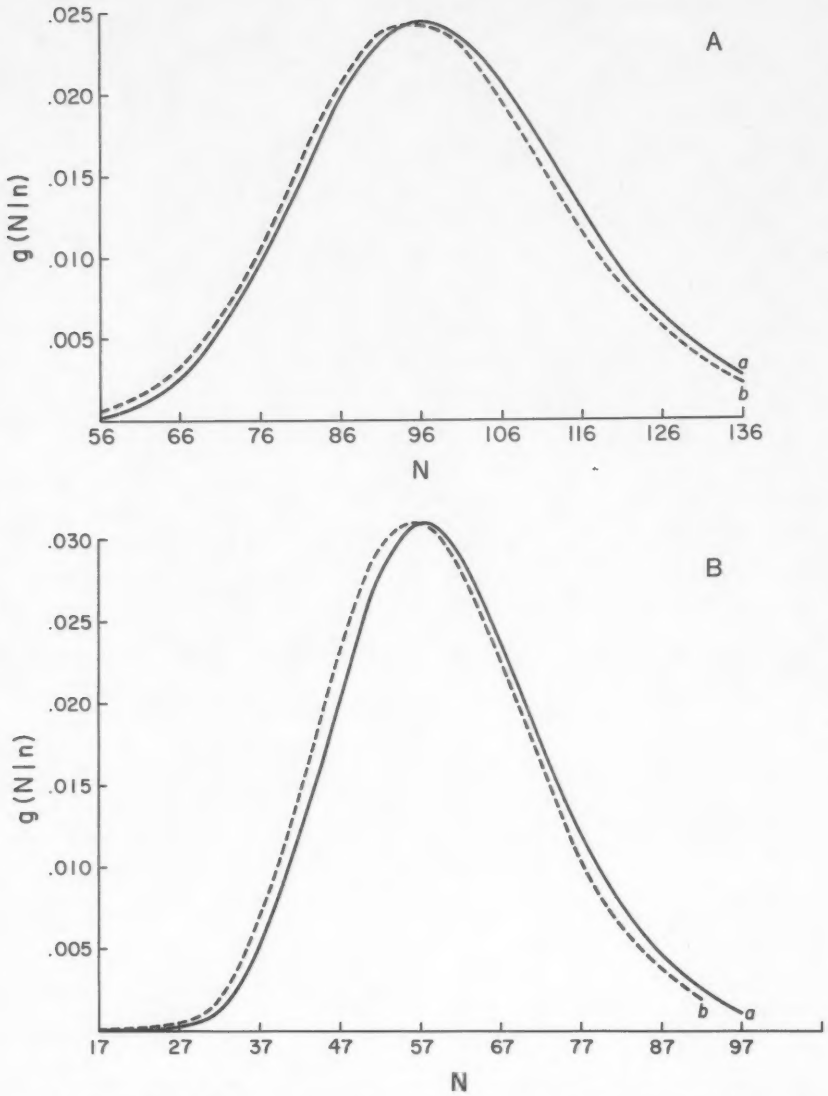


FIG. 1. Comparison of uniform (curve *a*) and noninformative priors (equation 2.22) (curve *b*) distributions on $N$. Parameter values: $\epsilon = 0.01$, $t = 30$, (A) $n = 25$, (B) $n = 15$.

Next consider the variable $Y = N - n$, which is the number of schools that remain. Since $\Pr\{Y = y\} = \Pr\{N = n + y\}$, equation (2.23) shows that

$$\Pr\{Y = y\} = \binom{n+y}{n} p^{n+1} q^y \tag{2.25}$$

$$= \binom{y+r-1}{y} p^r q^y \tag{2.26}$$

where $r = n + 1$. Consequently, the distribution of the remaining number of schools is negative binomial with parameters $r$ and $p$.

The noninformative prior (2.18) can be converted to a proper prior distribution if we fix a maximum value for $N$. Let $N_m$ be that value plus one. Then a proper noninformative prior $g(N)$ is given by

$$g_m(N) = \begin{cases} 1/(N_m + 1), & N = 0, 1, \ldots, N_m \\ 0 & \text{otherwise.} \end{cases} \tag{2.27}$$

Given that $n$ schools were observed, it is easily found from (2.17) that

$$g_m(N|n) = c \binom{N}{n} q^N, \quad N = n, n+1, \ldots, N_m \tag{2.28}$$

where the normalization constant is

$$c = \sum_{N=n}^{N_m} \binom{N}{n} q^N.$$

Other choices of the prior distribution $g(N)$ are possible, and

equation (2.17) can be tailored to the user's prior intuition about $N$ (an example of such intuition is discussed in section 3, see Fig. 5). Given a prior distribution, equation (2.24) can be used to construct a Bayes confidence interval for $N$ around $\hat{N}$. (If $k$ independent searchers operate, then $1 - e^{-\epsilon t}$ is replaced by $1 - e^{-k\epsilon t}$.)

Finally, consider predictions of future harvest (in the same season) given that $n$ schools were found in $(0, t)$. That is, if $s$ more units of search time elapse, what can be said about the statistics of the predicted catch? Let $H$ denote this catch. In light of (2.5), the conditional expectation and variance of the remaining harvest are

$$\begin{aligned} E\{H|\hat{N}, n, s\} &= (\hat{N} - n)(1 - e^{-k\epsilon s}) \\ \text{Var}\{H|\hat{N}, n, s\} &= (\hat{N} - n)(1 - e^{-k\epsilon s})e^{-k\epsilon s} \end{aligned} \tag{2.29}$$

so that the coefficient of variation of the remaining harvest is

$$\text{CV}\{H|\hat{N}, n, s\} = \frac{1}{\sqrt{\hat{N} - n}}\left[\frac{e^{-k\epsilon s}}{1 - e^{-k\epsilon s}}\right]^{1/2}. \tag{2.30}$$

Consider a fishery manager operating under an exogenous constraint on escapement of the following form: the stock level at the end of the season should be a fraction $f$ $(0 < f < 1)$ of the stock level at the start of the season. For the stochastic problem here, one can only calculate the probability that the stock level at the end of the season is greater than $f$ times the initial stock level. Suppose that $n$ schools have been caught after a search time $t$. Let $p(f, n, t, s, N)$ be the probability that at least $fN$ schools remain if there are $s$ more time units of search in the season, conditioned on $n$ and $N$. This probability is the same as the probability that the total harvest is less than $(1-f)N$, subject to the same conditioning. To find $p(f, n, t, s, N)$, introduce the random variable $n_s$ = number of schools caught in the next $s$ units of search time. The distribution of $n_s$ is binomial with parameters $N - n$ and $1 - e^{-k\epsilon s}$. Thus

$$\begin{aligned} p(f, n, t, s, N) &= \Pr\{n + n_s \leqslant (1 - f)N\} \\ &= \Pr\{n_s \leqslant (1 - f)N - n\} \\ &= \begin{cases} \displaystyle\sum_{m=0}^{(1-f)N-n} \binom{N-n}{m}(1 - e^{-k\epsilon s})^m(e^{-k\epsilon s})^{N-n-m} \\ \qquad\qquad \text{if } n \leqslant (1 - f)N \\ 0 \qquad\qquad \text{otherwise.} \end{cases} \end{aligned} \tag{2.31}$$

The actual harvest statistics must be averaged over the posterior distribution $g(N|n)$; i.e.

$$\begin{aligned} E\{H|n, s\} &= \sum_{N=n}^{\infty} g(N|n)E\{H|N, n, s\} \\ \text{CV}\{H|n, s\} &= \sum_{N=n}^{\infty} g(N|n)\,\text{CV}\{H|N, n, s\} \\ p(f, n, t, s) &= \sum_{N=n}^{\infty} g(N|n)p(f, n, t, s, N). \end{aligned} \tag{2.32}$$

An example showing how (2.32) is used is presented in the next section.

## 3. Estimating Stock Size in the Absence of Catch

Imagine a region in which some effort, measured by search time, is expended but no fish are caught. What can be said about the stock level in the region? This is a case in which the Bayesian approach is essentially the only one possible. One cannot rule out the presence of fish; instead the quantity that must be found is the posterior probability distribution for $N$, the number of aggregations in the region, when $n = 0$ schools were discovered during $t$ hours of search.

TABLE 2. An example showing confidence intervals ($n = 20$, $P = 0.05$, $\hat{N} = 400$).

| Confidence level ($\gamma$) | Range of $N$ |
|---|---|
| 0.85 | [339, 459] |
| 0.90 | [335, 465] |
| 0.95 | [331, 467] |
| 0.99 | [327, 471] |

Using the noninformative prior (2.18) (which is probably a good assumption if the region has never been fished before) gives the posterior density

$$g(N|0) = pq^N \quad N \geqslant 0 \tag{3.1}$$

where $p = 1 - e^{-k\epsilon t}$ and $q = 1 - p$.

In this case, the MLE for $N$ is $\hat{N} = 0$. Thus, the Bayesian confidence interval (2.24) is of the form $[0, J^*]$, where $J^*$ is the smallest integer such that

$$\sum_{N=0}^{J^*} g(N|0) \geqslant \gamma. \tag{3.2}$$

Since $g(N|0)$ is simply a geometric distribution, the sum in (3.2) is $1 - q^{J^*+1}$. Thus, (3.2) can be explicitly solved for $J^*$, giving

$$J^* = \left[\frac{\log(1 - \gamma)}{\log q}\right] - 1 = \left[\frac{\log(1 - \gamma)}{-k\epsilon t}\right] - 1 \tag{3.3}$$

where, as before, $[x]$ is the integer part of $x$.

If the proper noninformative prior (2.27) is used, the posterior distribution (2.28) turns out to be

$$\begin{aligned} g_m(N|0) &= \left\{\frac{p}{1 - q^{N_m+1}}\right\} q^N, \quad N = 0, 1, \ldots, N_m \\ &= 0 \qquad\qquad \text{otherwise.} \end{aligned} \tag{3.4}$$

A Bayesian confidence interval for $N$ is now constructed in the same way. It is of the form $[0, J_m^*]$, where $J_m^*$ is given by

$$J_m^* = \left[\frac{\log((1 - \gamma)(1 - q^{N_m+1}))}{\log q}\right] - 1. \tag{3.5}$$

Figures 2A and 2B show results of calculations using $p = 1 - e^{-k\epsilon t} = 0.1$, 0.01 and $N_m = 21$, 51. Table 3 shows the values of the Bayesian confidence intervals for $p = 0.1$. For $p = 0.01$, the 80, 90, and 95% confidence intervals are all of the form $[0, N_m]$. That is, so little time was expended that essentially nothing can be said about the stock size.

The theory presented thus far was based on the uniform prior. This need not be the case; e.g. Fig. 3 shows a "tent-like" distribution in which one can assert that the region is "good" (i.e. large stock level) with probability $\alpha_3$, "average" (moderate stock level) with probability $\alpha_2$, and "bad" (low stock level) with probability $\alpha_1 = 1 - \alpha_2 - \alpha_3$. Thus, this theory can incorporate any intuition that a manager has about the region of interest.

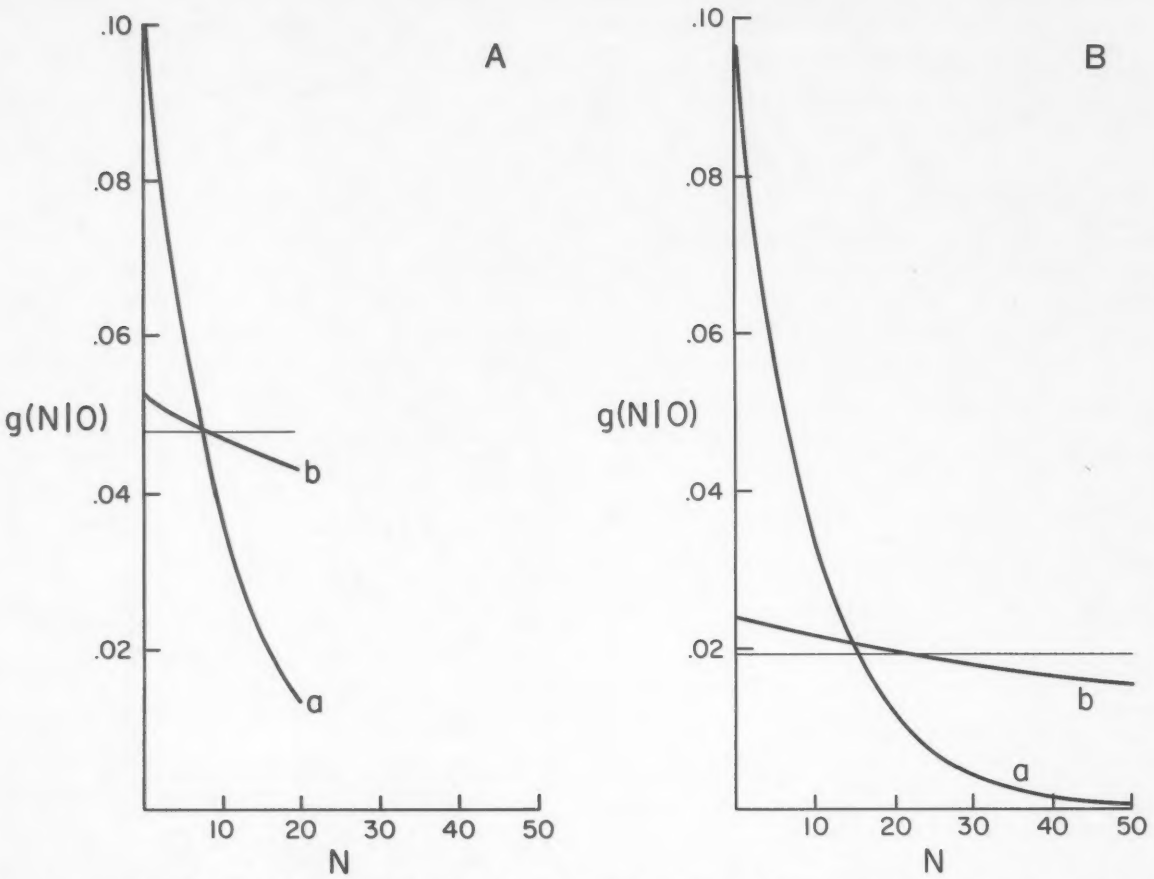


FIG. 2. Posterior distribution $g(N|0)$ when (A) $N_m = 21$ and (B) $N_m = 51$ and the probability of finding a school, given that it is present, is 0.10 (curve *a*) or 0.01 (curve *b*). The uniform prior $g_m(N)$ is also shown (straight line).

TABLE 3. Confidence intervals on stock size in the absence of catch.

| | Confidence interval for | | |
|---|---|---|---|
| $N_m$ | $\gamma = 0.8$ | $\gamma = 0.85$ | $\gamma = 0.90$ |
| 21 | [0, 15] | [0, 18] | [0, 20] |
| 51 | [0, 14] | [0, 17] | [0, 20] |

## 4. Real Time Determination of the Length of Fishing Seasons

In this section, it is shown how the theory developed in section 2 could be used to provide a real time, adaptive determination of the length of fishing seasons. That is, imagine a situation in which the length of the season is not set in advance, but is determined as the season progresses. How should one determine the length of the rest of the season?

The basic idea is that as the stock is depleted, the time between discoveries of schools will increase. Consequently, by using the theory of section 2, one can estimate stock size from search times. The underlying assumptions are then (1) independent and random search by fishing vessels and (2) no recruitment during the season.

The ideas developed in section 2 are best illustrated by a simulation. The details of the simulation program are discussed in the Appendix. In summary, this simulated fishery lasts for up to 10 periods. The manager has the discretion, at the end of each period, to determine how much longer the fishery remains open. There are $k = 15$ vessels participating in the fishery, and $\epsilon = 0.01$. Each of three years simulated shows a pronounced decrease in catch (Fig. 4), presumably related to the depletion of the stock, but fluctuations are considerable. Table 4 shows the 25-yr averages of the catch and the coefficient of variation of the catch.

It is assumed that the manager can estimate accurately the catch in each period and the total time required to discover the fish that were set upon. This time, for instance, could be the total time at sea minus the total set time. (The catch can be estimated from landings and the search time from trip reports; see the next section.) It is also assumed that the manager operates under an exogenous biological constraint that the stock at the end of the season should be no less than a fraction $f$, say $f = 0.2$–$0.4$, of the stock at the beginning of the season. The difficult part of the decision, of course, is that the stock at the start of the season can only be estimated as data obtained throughout the season.

With this information, the following quantities are computed using the theory of section 2: (1) the maximum likelihood

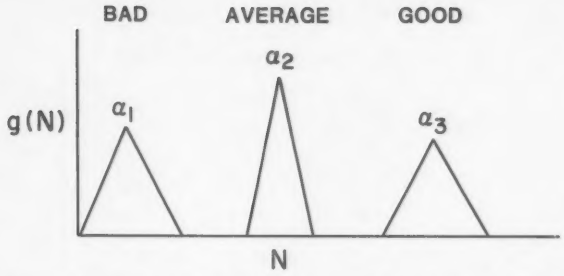


FIG. 3. Proposed prior distribution that can be used when there is a probability $\alpha_1$ that the region is bad, $\alpha_2$ that the region is average, and $\alpha_3$ that the region is good.

estimation for the number of schools at the start of the season, $\hat{N}$, and (2) the posterior distribution for $N$, given the data.

For each choice of $N$, the expectation and variance in the catch if the season remains open for $T$ more periods are calculated. Here, $T$ runs between 1 and the maximum number of periods possibly remaining in the season. For a given $T$, the probability that the stock remains above $fN$ if the season lasts $T$ more periods is calculated. The calculations are then averaged over $N$ and the results presented in tabular form. The theory for this procedure is given in equations (2.29)–(2.32).

To illustrate the results, consider the following data for the first three periods of a new season:

| Period | Catch (relative units) | Search time (relative units) |
|---|---|---|
| 1 | 21 | 1 |
| 2 | 11 | 1 |
| 3 | 15 | 1 |

When the theory is applied after the first period of fishing, the maximum likelihood value for the initial number of schools is $\hat{N} = 150$. Results for the rest of the season using the uniform prior (Table 5) indicate that at least one more period of fishing can be allowed without any danger to the stock. In the second period, 11 schools are caught. Thus, for the first two periods, the total catch is 32 schools. This gives $\hat{N} = 123$. The corresponding results for the rest of the season (Table 6) again indicate little chance of damage to the stock of the season if the fishery is open one more period. In the third period, 15 schools are caught; this gives 47 schools for the first three periods and $\hat{N} = 129$. The corresponding results are shown in Table 7. This procedure is repeated until either 10 periods of fishing elapse or the probability of damage to the stock becomes sufficiently high to warrant closure.

Figure 5 shows how the expected seasonal catch changes as information is gathered during the first three periods. Figures 6A and 6B show the probability that the stock level is above $fN$ at the end of the season. These results appear to be less sensitive to the additional weekly information than the total catch is.

In a real fishery, it is likely that the data are noisier, but the methods described here can still be useful as a tool for deciding about season closures.

Other management schemes can be used with this approach. For example, many fisheries operate with a targeted escapement level. Suppose that $N_s$ is the escapement level and that $\hat{N}$ is the MLE for $N$, given that $n$ schools were encountered in search time $t$. Then there remain $\hat{N} - n$ schools, and a search effort of $\hat{t}$ hours will lead to the estimated expected catch $(\hat{N} - n)$

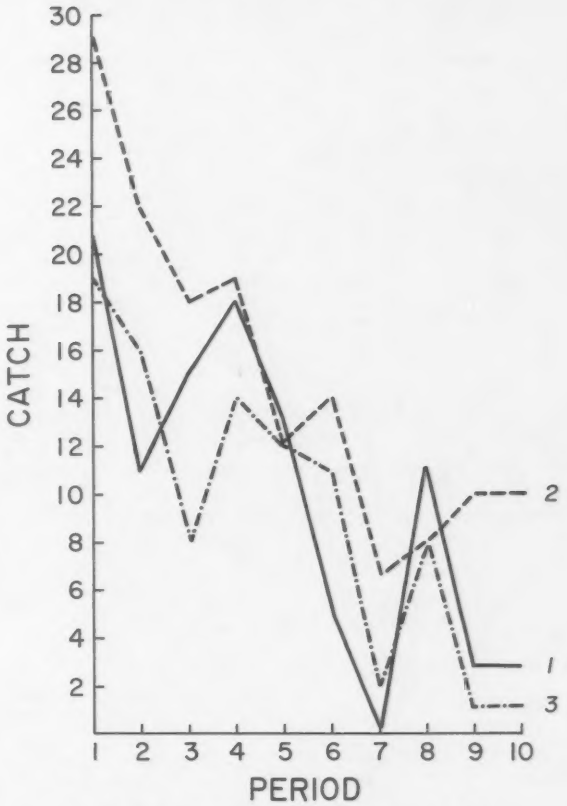


FIG. 4. Catch for three years in the simulated fishery.

TABLE 4. Historical 25-yr catch rate (relative units) for the simulated 10-period fishery.

| Period | Average | Coefficient of variation |
|---|---|---|
| 1 | 19.8 | 0.263 |
| 2 | 17.4 | 0.275 |
| 3 | 14.4 | 0.359 |
| 4 | 12.0 | 0.235 |
| 5 | 10.3 | 0.299 |
| 6 | 9.64 | 0.296 |
| 7 | 7.60 | 0.423 |
| 8 | 6.80 | 0.311 |
| 9 | 5.92 | 0.468 |
| 10 | 4.76 | 0.368 |

$(1 - \exp(-k\hat{e}\hat{t}))$ where $k$ is the number of vessels in the fishery. The value of $\hat{t}$ can be determined so that the targeted escapement is reached. That is, if it exists, $\hat{t}$ is the positive solution of the following equation:

$$(4.1) \qquad N_s = (\hat{N} - n)e^{-k\hat{e}\hat{t}}.$$

Equation (4.1) will not have a solution if either $\hat{N} = n$ (see section 2) or $N_s \geq \hat{N} - n$. The latter indicates that the escapement level may not be attainable. In either case, if (4.1) does not have a positive solution, then the season should be closed immediately.

TABLE 5. Results using catch data from the first period ($n = 21$, $t = 1$, $\hat{N} = 150$).

| No. of extra periods in season | Predictions: Expected seasonal catch | CV in seasonal catch | Averaged Prob{stock > $fN$}: $f = 0.2$ | $f = 0.3$ |
|---|---|---|---|---|
| 1 | 39 | 0.031 | >0.9999 | 0.9994 |
| 2 | 55 | 0.039 | >0.9999 | 0.9967 |
| 3 | 68 | 0.043 | 0.9997 | 0.9859 |
| 4 | 80 | 0.044 | 0.9982 | 0.9816 |
| 5 | 90 | 0.045 | 0.9921 | 0.8672 |
| 6 | 98 | 0.044 | 0.9716 | 0.7089 |
| 7 | 106 | 0.043 | 0.9175 | 0.4881 |
| 8 | 112 | 0.041 | 0.8059 | 0.2626 |
| 9 | 118 | 0.039 | 0.6283 | 0.0993 |

TABLE 6. Results using catch data from the first two periods ($n = 32$, $t = 2$, $\hat{N} = 132$).

| No. of extra periods in season | Predictions: Expected seasonal catch | CV in seasonal catch | Averaged Prob{stock > $fN$}: $f = 0.2$ | $f = 0.3$ |
|---|---|---|---|---|
| 1 | 45 | 0.037 | >0.9999 | 0.9989 |
| 2 | 56 | 0.046 | 0.9999 | 0.9927 |
| 3 | 66 | 0.051 | 0.9992 | 0.9664 |
| 4 | 73 | 0.053 | 0.9951 | 0.8868 |
| 5 | 80 | 0.053 | 0.9778 | 0.7198 |
| 6 | 87 | 0.052 | 0.9238 | 0.4792 |
| 7 | 92 | 0.050 | 0.8030 | 0.2426 |
| 8 | 96 | 0.049 | 0.6080 | 0.0860 |

A more complicated procedure for determining the remaining length of the season is to find the positive $\hat{t}(N)$ that solves

$$N_s = (N - n)e^{-k\hat{e}\hat{t}} \tag{4.2}$$

and then define $\hat{t}$ by

$$\hat{t} = \sum_{N=n+1}^{\infty} g(N|n)\hat{t}(N). \tag{4.3}$$

Observe, however, that (4.1) and (4.3) give total remaining search time, and not total fishing time. One needs an algorithm that relates total fishing time to search time. Such an algorithm is described, for a particular fishery, in the next section.

## 5. Empirical Study of Pacific Ocean Perch (POP) near Rennell Sound, British Columbia

Rennell Sound is located on the west side of Graham Island in the Queen Charlotte Islands, British Columbia. The data on POP catch near Rennell Sound are nearly ideal for an empirical study of the usefulness of the search methods. First, the POP there is essentially a closed population, apparently the isolated remains of a once much more predominant stock (R. Stanley, Pacific Biological Station, Nanaimo, B.C., pers. comm.). There is little recruitment, so that the fishery is, in this case, exploiting an exhaustible resource. Second, the data set is sufficiently large to be broken into a subset for estimation of parameters and one for testing the methods. Third, the entire fishable area of the Sound is known (Leaman and Nagtegaal 1982). Fourth, the area was relatively unknown when first exploited. This means that the assumption of random search has considerable validity. Further discussion about the POP stock in Rennell Sound can be found in Leaman and Nagtegaal (1982), Nagtegaal et al. (1980), and Stocker (1981).

TABLE 7. Results using catch data from the first three periods ($n = 47$, $t = 3$, $\hat{N} = 129$).

| No. of extra periods in season | Expected seasonal catch | CV in seasonal catch | Averaged Prob{stock > $fN$}: $f = 0.2$ | $f = 0.3$ |
|---|---|---|---|---|
| 1 | 59 | 0.038 | >0.9999 | 0.9971 |
| 2 | 69 | 0.049 | 0.9998 | 0.9799 |
| 3 | 77 | 0.053 | 0.9983 | 0.9108 |
| 4 | 84 | 0.055 | 0.9886 | 0.7385 |
| 5 | 91 | 0.055 | 0.9481 | 0.4727 |
| 6 | 96 | 0.055 | 0.8372 | 0.2176 |
| 7 | 101 | 0.053 | 0.6356 | 0.0658 |

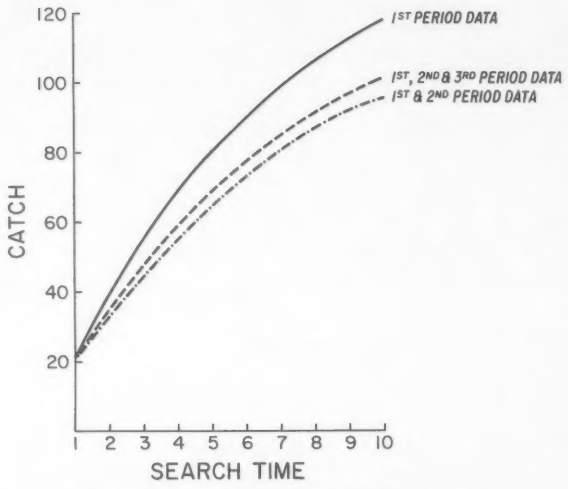


FIG. 5. Predicted catch as information is obtained.

The nature of search for POP aggregations may not fit all of the assumptions, particularly that an aggregation is fished out upon discovery. However, it will be seen that the assumptions are not violated too strongly, since the predictions based on the theory turned out to be reasonably accurate.

POP were first exploited near Rennell Sound in 1976. They are caught mainly when they form aggregations during the daylight. The log-book data kept at the Pacific Biological Station, Nanaimo, B.C., were used as a source of catch and effort information with the following rules:

(1) Each trip report was assumed to represent the encounter of one vessel with one aggregation of POP. The validity of this assumption is unknown. Given the type of log-book data available, this assumption (made for convenience) seems reasonable.

(2) The number of hours available for search was computed according to

$$\text{Search time} = \text{Days fished} - \text{set time} - \text{dark hours}. \tag{5.1}$$

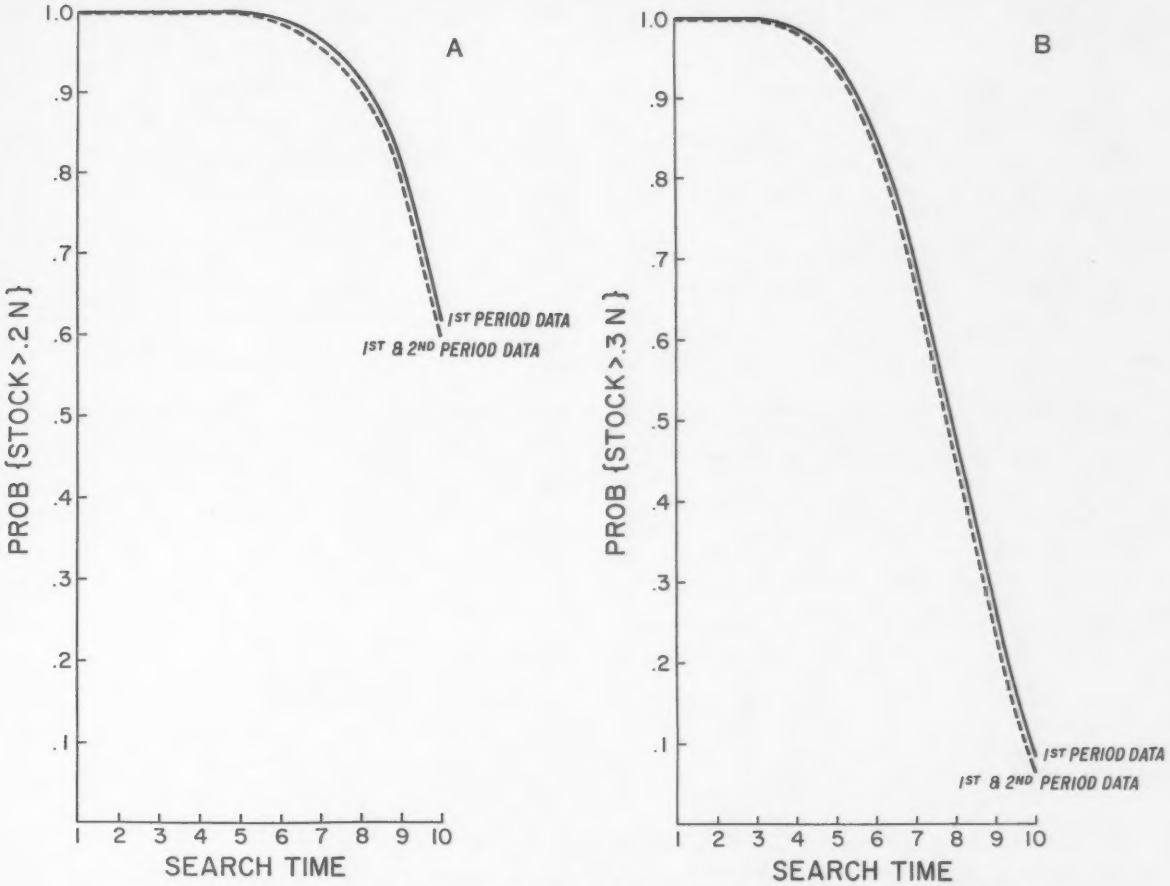


FIG. 6. Probability that the stock at the end of the season is greater than (A) 0.2 and (B) 0.3 of the initial stock.

Dark hours were computed using sunrise/sunset tables from an almanac.

By using equation (5.1) to compute search times, one implicitly assumes that fishing and searching are the only activities. If skippers logged the actual search time, then equation (5.1) would not be needed and one could find search time through dockside interviews.

For the empirical study of POP, the definition of $\epsilon$ is

$$\epsilon = \frac{vW}{A} \tag{5.2}$$

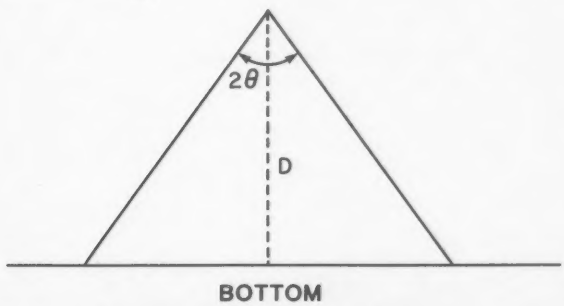


FIG. 7. Computation of the sweep width $W$.

where $v$ is the speed of the vessel, $W$ is the sweep width of the echosounder used in the search for fish, and $A$ is the fishable area. Leaman and Nagtegaal (1982) presented data on the trawlable area in Rennell Sound as a function of interval depth. Their results are shown below:

| Code | Depth interval (m) | Area (nautical miles$^2$) | % of total area |
|---|---|---|---|
| 1 | 164–218 | 26.92 | 40 |
| 2 | 219–272 | 6.10 | 9 |
| 3 | 273–327 | 7.24 | 11 |
| 4 | 328–382 | 7.27 | 11 |
| 5 | 383–437 | 5.85 | 9 |
| 6 | 438–491 | 7.69 | 12 |
| 7 | 491–547 | 5.32 | 8 |

A different $\epsilon$ was calculated for each depth interval.

The sweep width $W$ was calculated as follows (see Fig. 7). Imagine that the bottom is $D$ metres below the sounder and that the sounder ensonifies an angle of $2\theta$ below it. The ensonified width on the bottom is then

$$W = 2D \tan \theta. \tag{5.3}$$

(A more rigorous calculation, using the lateral range curve

(Koopman 1980), gives the same result, if it is assumed that the probability of detection within the triangle is 1.) The value of $\theta = 15°$ was used.

The following objectives were investigated:

(1) To use the data from January to June 1977 to estimate (a) the initial number of aggregates present, (b) confidence intervals on the initial number of aggregates, (c) biomass per aggregate, and (d) initial biomass and confidence intervals on the biomass using total biomass = (number of aggregates) × (biomass per aggregate).

(2) To predict catch as a function of effort from July 1977 through 1982, using both point estimates and confidence intervals.

(3) To investigate how the uncertainty in the estimate of biomass per aggregate affects the ultimate estimates of confidence intervals.

The data from January to June 1977 consist of 13 trip reports. For lack of any better identification procedure, it was assumed that each trip report corresponded to an encounter with one aggregation. The total search time was 181 h. The estimate for the initial number of aggregates, averaged over the seven depth intervals, is $\hat{N} = 646$ aggregates. That is, observe from (2.16) that the estimate $\hat{N}$ depends upon $\epsilon$; one should write $\hat{N}(\epsilon)$. The ultimate estimate of $\hat{N}$ is then the average of $\hat{N}(\epsilon)$ over $\epsilon$: $\hat{N} = E_\epsilon(\hat{N}(\epsilon))$ where $E_\epsilon$ denotes the expectation over $\epsilon$, using the data shown below (5.2) (an incorrect method would be to use (2.16) with $\epsilon$ replaced by its average value). The average catch per encounter (i.e. per trip report) was $\hat{B}_A = 32$ tons, and the standard deviation was 22 tons (the resulting coefficient of variation is 0.69). In what follows (until the final discussion in this section), the 32 tons per aggregate will be treated as a point estimate. Finally, the average catch per set for the initial data was 2.4 tons set (with a 1-h nominal set time). It is assumed here that when a school is encountered, it is completely fished out — even if this requires more than one set. Since the theory uses search time only, there is no problem with multiple sets, as long as the appropriate corrections for times are used (as in equation (5.1)).

The estimate for the initial biomass is defined by

$$\hat{B}_0 = \hat{N}\hat{B}_A \tag{5.4}$$

where $\hat{B}_A$ is the 32 tons per aggregate and $\hat{N}$ is the averaged initial number of aggregates. Three point estimates were constructed, using the lowest, midpoint, and greatest depth for each depth interval. These results are

$$\hat{B}_0 = \begin{cases} 23\,411 \text{ tons (lowest depth)} \\ 20\,731 \text{ tons (midpoint)} \\ 18\,646 \text{ tons (greatest depth).} \end{cases}$$

In all other calculations, only the midpoint of the depth interval was used. Note, however, that just switching the depth used in the sweep width calculation can lead to differences of 10–13% in biomass estimates. Stock surveys gave estimates of about 20 000 tons (B. Leaman, Pacific Biological Station, Nanaimo, B.C., pers. comm.).

Bayesian confidence intervals on $N$ were constructed as described in section 2, using an improper uniform prior.

The 90% confidence intervals are

Number of aggregations: 516–776

Biomass: 16 512 – 24 832 tons.

The 95% confidence intervals are

Number of aggregations: 508–786

Biomass: 16 256 – 25 152 tons.

It should be stressed that these confidence intervals treat the biomass per aggregate as fixed. It will be seen that if one includes the uncertainty in the biomass per aggregate, then the width of the confidence interval increases considerably. It is worth noting that if the depths were aggregated, so that only one value of $\epsilon$ (averaged over the seven depth intervals) was used, the resulting estimates are 451–677 aggregates and 14 832 – 21 664 tons for the 90% interval and 443–685 aggregates and 14 176 – 21 920 tons for the 95% interval. These are about 13% too low, relative to the proper procedure of estimating $\hat{N}$ conditioned on $\epsilon$ and then averaging over $\epsilon$.

Next, predictions were made for catches from July 1977 to 1982. The predictions were computed as follows. First, since the average size of an aggregate is 32 tons and the catch per set is 2.4 tons, there are about 13 sets per aggregate encountered, or 13 h of fishing per aggregate at the nominal value of 1 h per set. Suppose that $N_R$ aggregates remain and that the total daylight effort will be $T_E$. Suppose $t_s$ hours will be spent searching. The expected number of aggregates yet to be found is $N_R(1 - e^{-\epsilon t_s})$. The amount of time spent fishing will be 13 times this. Thus, $t_s$ satisfies

$$t_s + 13N_R(1 - e^{-\epsilon t_s}) = T_E. \tag{5.5}$$

Solving this equation for $t_s$ gives the search time, and from that the catch. This search time actually depends upon $N_R$, so that if $N_R$ has a distribution, so does the search time. For simplicity, the search time was calculated using the maximum likelihood estimate for $N_R$ only (initially, $N_R = \hat{N} - 13$). Bayesian confidence intervals for the predicted catch (around the expected catch of $N_R(1 - e^{-\epsilon t_s})$ aggregates × 32 tons aggregate) were constructed using a modification of the method described in section 2. Table 8 shows the point estimate for catch, the 90% confidence interval, and the actual catch observed from July 1977 onward. With the exception of 1978, the predicted and observed catches agree in the sense that the actual catch was either in the confidence interval (July–December 1977, 1980, and 1981) or very close to it (1981). The anomalous year 1978 was at least partially explained by a further investigation of the data (Mangel 1983) which shows that a number of vessels entered the Rennell Sound fishery briefly, exerted effort, obtained little or no catch, and exited. In such a situation, one expects that the predicted catch will be larger than the actual catch, which was indeed the case.

The confidence intervals in Table 8 are too small, for two reasons. First, the distribution in the number of aggregates should be reflected in a distribution on the search times. This

TABLE 8. Predicted and observed POP catches, 1977–82.

| Year[a] | Effort $T_E$ (daylight hours) | Point estimate (tons) | Catch 90% confidence interval | Actual |
|---|---|---|---|---|
| July–Dec. 1977 | 280 | 325 | [179, 468] | 430 |
| 1978 | 240 | 279 | [154, 403] | 119 |
| 1980 | 47 | 41 | [9, 77] | 51 |
| 1981 | 48 | 45 | [13, 77] | 43 |
| 1982 | 48 | 45 | [13, 77] | 79 |

[a]There were no substantial POP sets in 1979.

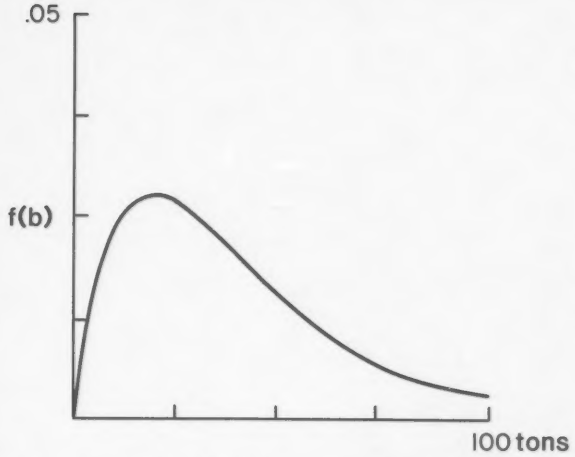


FIG. 8. Biomass density for biomass per aggregate $f(b) = 0.063^2 \exp[-0.063b]$.

calculation was not done, and only average predicted search times were used, because it is not clear that the quality of the data warrants such a calculation (this is an ex post facto prediction). In a real problem, i.e. if one were actually trying to predict future catches, the distribution on search times would need to be considered. Second, the uncertainty in the biomass per aggregate was not taken into account. In principle, the uncertainty in biomass per aggregate can be accounted for as follows. Let $f(b)$ be the probability density of $B_A$, the biomass per aggregate. Experience suggests that the distribution should be skewed so that the peak of the density occurs at a biomass $b$ that is less than the mean biomass. One choice is the gamma density:

$$(5.6) \qquad f(b) = \frac{\alpha^\nu e^{-\alpha b} b^{\nu-1}}{\Gamma(\nu)}$$

with mean $\nu/\alpha$ and coefficient of variation $1/\sqrt{\nu}$. Matching these to 32 tons and 0.69, respectively, gives

$$(5.7) \qquad \nu = 2.1, \qquad \alpha = 0.067.$$

For ease of calculation, $\nu = 2$ and $\alpha = 0.063$ will be used in the calculations that follow. Figure 8 shows the density $f(b)$. Observe how the curve is skewed to the left. Differentiation of (5.6) shows that the maximum value of $f(b)$ occurs at

$$(5.8) \qquad b^* = \frac{\nu - 1}{\alpha}$$

which is 16.4 tons (exactly) or 15.9 tons (in the approximation used for calculation) per aggregate, rather than the point estimate of 32 tons.

Now the total biomass, $B$, is given by

$$B = \sum_{i=1}^{N} B_i,$$

where $B_i$ is the biomass of the $i$th aggregate. To compute the probability density of $B$, an assumption must be made about the mechanism of aggregation. The two bracketing assumptions are the following ones:

(1) The biomasses of the aggregates are independent random variables with probability density given by (5.6).

(2) All aggregates are identical and have the same biomass, which is unknown. The frequency density of the unknown biomass is assumed to be given by (5.6).

If assumption (1) is correct, then the total biomass is given by the sum of $N$ independent random variables, each of which has a gamma distribution with parameters $\nu$ and $\alpha$. It is easily shown (by use of the moment generating function, which is

$$\phi(t) = \left(\frac{\alpha}{\alpha - t}\right)^\nu$$

for a gamma distribution with parameters $\nu$ and $\alpha$) that conditioned on $N$, the total biomass $B$ has a gamma density with parameters $N\nu$ and $\alpha$. Consequently,

$$(5.9) \qquad f_B(m)dm = \Pr\{m \leq B \leq m + dm\} = \sum_{N \geq n_s} \frac{\alpha^{N\nu} e^{-\alpha m} m^{N\nu-1}}{\Gamma(N\nu)} g(N|n_s)dm$$

where $g(N|n_s)$ is the posterior probability that $N$ aggregates were initially present, given that $n_s$ aggregates were found in time $t_s$ (here $n_s = 13$ and $t_s = 181$ h). Since the coefficient of variation of the gamma density is $1/\sqrt{\nu}$, the density (5.5) becomes more and more sharply peaked around the mean as $\nu$ increases. This means that confidence intervals based on (5.9) will be similar to those already presented. (We plan to provide a more complete discussion of confidence intervals based on (5.9) in a subsequent paper.)

If assumption (2) is correct, the density for the total biomass is given by

$$(5.10) \qquad f_B(m)dm = \Pr\{m \leq B \leq m + dm\} = \Pr\{m \leq NB_A \leq m + dm\}$$

where $N$ is the number of aggregates initially present. This equation is rewritten as

$$(5.11) \qquad \Pr\{m \leq NB_A \leq m + dm\} = \sum_{N \geq n_s} \Pr\left\{\frac{m}{N} \leq B_A \leq \frac{m + dm}{N}\right\} g(N|n_s) = \sum_{N \geq n_s} f\left(\frac{m}{N}\right) g(N|n_s) \frac{dm}{N}.$$

Using the density (5.6) with parameters (5.8) in (5.11) gives

$$(5.12) \qquad \Pr\{m \leq B \leq m + dm\} = \sum_{N \geq 13} (0.063)^2 \exp\left[\frac{-0.063m}{N}\right]\left(\frac{m}{N}\right) g(N|13) \frac{dm}{N}.$$

In this equation, $g(N|13)$ is given by the "negative binomial" posterior distribution (2.23) for the initial number of schools, given that $n = 13$ aggregations were found in $t = 181$ h. The distribution in (5.12) is easily computed on a desktop microcomputer. Figure 9 shows the biomass estimate computed from equation (5.12). (Actually, the calculation is somewhat more complex, since $g(N|13)$ must first be conditioned on the depth level, the biomass computed, and then averaged over all the depths.) The biomass was truncated at 52 000 tons.

The peak of the curve occurs at 9000 tons and the numerically computed mean is 19 909 tons (this mean is less than the point estimate 20 731 tons because of truncation of the density at 52 000 tons). The confidence intervals around the mean and the

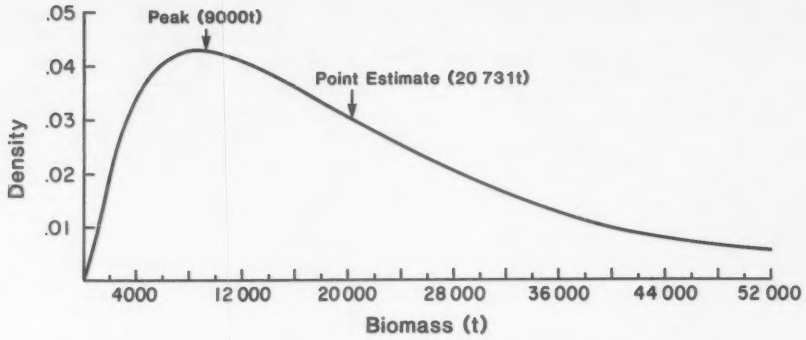


FIG. 9. Estimated biomass density function for POP under assumption (2) about aggregation.

maximum are shown below:

| Confidence level | Around | |
|---|---|---|
| | Mean | Maximum |
| 85% | [3000, 36 000] tons | [0, 29 500] tons |
| 90% | [1000, 38 000] tons | [0, 36 500] tons |

These confidence intervals are much larger than those obtained when a point estimate of the biomass per aggregate is used. The great width of the confidence interval is caused, in large part, by the choice of the gamma distribution. That is, the long, slowly decaying tails of the gamma density lead to the long tails in the biomass distribution and thus the large confidence intervals.

One implication is clear, however, and it is that knowledge of distribution of the biomass per aggregate and the mechanism of aggregation are important if one wants meaningful confidence intervals. This point cannot be stressed too greatly. There is need for biological research to estimate the distribution of biomass per aggregate. With such large confidence intervals, a cautious management program is probably justified.

In conclusion, it is worthwhile to consider the "design of experiment" question. That is, what are the ideal data for an analysis such as this one? What data would be needed to make the analysis described here extremely accurate and as bias free as possible?

Some of the data that could be collected, but currently are not, are the following:

(1) The actual cycle of search–fish–search. If the fisherman recorded the actual search times, followed by fishing time, followed by search time, etc., then the search time would be known precisely.

(2) Fishing the same aggregation. Often the fishermen will encounter an aggregation, fish it for a while, follow it, and then fish it again. If the fishermen made a notation of such instances, it would be possible to eliminate another bias in the analyses. In another instance, schools may be partially fished by one vessel, and at some later point set upon by a different vessel. If one can estimate the probability of this occurrence and the fraction of a school taken on a set, then the theory could be easily modified accordingly (e.g. see Mangel and Clark 1983).

(3) Distribution of biomass per aggregate. If the actual distribution of biomass per aggregate were known (either from separate biomass surveys or from substantial analyses of catch data), then a calculation similar to equation (5.11) could be performed, with more confidence in the results.

## 6. Concluding Comments

All calculations reported in this paper were done on a desktop microcomputer. This means that the techniques are feasible for fishery managers and fishermen, who are becoming accustomed to the use of small computers in planning fishery operations. Software for the theory in section 2 is easily developed. A number of extensions of the theory presented here are currently under investigation. The first is that recruitment is not taken into account in the current theory. This is not a problem if one is interested in only a single season which is short enough so that recruitment is not significant, or the stock of interest has essentially independent generations (e.g. shrimp). However, the theory developed here can be extended to include recruitment. The second limitation is that schools of fish are typically clumped and that the theory developed here does not take clumping explicitly into account. One can do this by putting additional distributions on $N$ or $\epsilon$ in the basic search model. This adds no additional conceptual, and very little computational, difficulty, however. A third limitation is that learning by fishermen is not taken into account. This learning has two major components. The first is local, nonrandom search. That is, after discovering a school, a vessel may execute a local, exhaustive (nonrandom) search about its find. (Tuna vessels seem to operate this way (T. Smith, NMFS-Southwest Fisheries Center, La Jolla, CA, pers. comm.).) Thus, one has two kinds of searches: random searches for "patches" (the first school found) followed by nonrandom searches within patches. The second component of learning involves learning how to fish the ground. That is, the value of $A$ in (2.4) pertains to the entire fishing ground. As the fishermen search, they learn unprofitable areas of the ground. Thus $A$ decreases, but the rate at which it decreases is unknown. For example, one could replace (2.4) by

$$(6.1) \qquad \epsilon = \epsilon(t) = \frac{Wv}{A(t)}$$

where

$$(6.2) \qquad A(t) = \frac{A_0}{1 + \theta t}$$

and $A_0$ is the initial size of the ground (physical size) and $\theta$ is the

learning rate. If such a procedure is followed, the basic result (2.5) is replaced by

$$(6.3)\quad \Pr\{k \text{ searchers discover } n \text{ schools in } (0, t)\} = \binom{N}{n}\left[1 - \exp\left(-\frac{ktWv}{A_0} - \frac{\theta kt^2Wv}{A_0}\right)\right]^n \times \left[\exp\left(-\frac{ktWv}{A_0} - \frac{\theta kt^2Wv}{A_0}\right)\right]^{N-n}.$$

The problem now is to estimate $N$ and $\theta$, which is equivalent to simultaneously estimating $N$ and $p$ in the binomial formula

$$\binom{N}{n} p^n (1-p)^{N-n}.$$

It is easily shown that maximum likelihood estimates give the result $\hat{N} = n$, $\hat{p} = 1$. One can however, use Bayesian methods to update a joint density for $N$ and $p$. Such methods are currently being developed.

## Acknowledgments

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## References

ALLEN, R., AND R. PUNSLY. 1984. Catch rates as indices of abundance of yellowfin tuna, *Thunnus albcares*, in the eastern Pacific Ocean. Bull. Int. Am. Trop. Tuna Comm. 18: 303–379.

BLUMENTHAL, S, AND R. C. DAHIYA. 1981. Estimating the binomial parameter *n*. J. Am. Stat. Assoc. 76: 903–909.

BOX, G. E. P., AND G. C. TIAO. 1973. Bayesian inference in statistical analysis. Addison-Wesley, Reading, MA. 588 p.

BUTTERWORTH, D. S. 1982. On the functional form used for $g(y)$ for Minke Whale sightings, and bias in its estimation due to measurement inaccuracies. Rep. Int. Whaling Comm. 32: 883–888.

CLARK, C. W., AND M. MANGEL. 1979. Aggregation and fishery dynamics: a theoretical study of schooling and the purse-seine fishery. U.S. Fish. Bull. 77: 317–337.

COOKE, J. 1984. On the relationship between catch per unit effort and whale abundance. Rep. Int. Whaling Comm. 35. (In press)

DELURY, B. 1947. On the estimation of biological populations. Biometrics 3: 145–167.

1951. On the planning of experiments for the estimation of fish populations. J. Fish. Res. Board Can. 8: 281–307.

FELLER, W. 1968. An introduction to probability theory and its applications. Vol. 1. Wiley, New York, NY. 509 p.

GOUDIE, I. B. J., AND C. M. GOLDIE. 1981. Initial size estimation for the linear pure death process. Biometrika 68: 543–550.

KOOPMAN, B. O. 1980. Search and screening. Pergamon Press, New York, NY. 368 p.

LEAMAN, B. M., AND D. A. NAGTEGAAL. 1982. Biomass estimates of rockfish stocks off the West Coast of the Queen Charlotte Islands during 1978 and 1979. Can. MS Rep. Fish. Aquat. Sci. 1652: 46 p.

MANGEL, M. 1982. Search effort and catch rates in fisheries. Eur. J. Oper. Res. 11: 361–366.

1983. Stock assessment in highly aggregated fisheries. Final report on California Sea Grant Project NOAA BOAA-D-00120: 27 p.

MANGEL, M., AND C. W. CLARK. 1983. Uncertainty, search and information in fisheries. J. Cons. Cons. Int. Explor. Mer 41: 93–103.

MARTZ, H. F., AND R. A. WALLER. 1982. Bayesian reliability analysis. Wiley, New York, NY. 744 p.

NAGTEGAAL, D. A., G. A. THOMAS, AND B. M. LEAMAN. 1980. Catches and trawl locations of M/V Blue Waters during rockfish exploration and assessment cruises to the west coast of the Queen Charlotte Islands and the northwest coast of Vancouver Island in 1978. Can. Data Rep. Fish. Aquat. Sci. 218: 103 p.

NEYMAN, J. 1949. On the problem of estimating the number of schools of fish. Univ. Calif. Publ. Stat. 1: 21–36.

OLKIN, I., A. J. PETKAU, AND J. V. ZIDEK. 1981. A comparison of *n* estimates for the binomial distribution. J. Am. Stat. Assoc. 76: 636–642.

PALOHEIMO, J. E. 1971. A stochastic theory of search: implications for predator–prey situations. Math. Biosci. 12: 105–132.

ROTHSCHILD, B. 1972. An exposition on the definition of fishing effort. U.S. Fish. Bull. 70: 671–679.

1977. Fishing effort, p. 96–115. *In* J. Gulland [ed.] Fish population dynamics. Wiley, New York, NY.

SEBER, G. A. F. 1982. The estimation of animal abundance. Macmillan Publishing Co., New York, NY. 654 p.

STOCKER, M. [ED.] 1981. Groundfish stock assessments off the west coast of Canada in 1981 and recommended total allowable catches in 1982. Can. MS Rep. Fish. Aquat. Sci. 1626: 282 p.

WASHBURN, A. 1981. Search and detection. Military Applications Section, Operations Research Society of America, Arlington, VA. 127 p.

WILEN, J. E. 1979. Fisherman behavior and the design of efficient fisheries regulation programs. J. Fish. Res. Board Can. 36: 855–858.

## Appendix: Description of the Simulation Program for Catch Data

The program used to generate data for the analysis in the text picks the initial number of schools, $N_0$, at the start of a season as follows. A random number, $m$, that is uniformly distributed on [100, 200] is drawn. Then $N_0$ is picked to be the integer part of $m$.

Given $N_0$, the catch in period $l$ is assumed to be binomial with parameters

$$N_0 - \sum_{i=1}^{l-1} Y_i \quad \text{and} \quad 1 - e^{-k\epsilon t}.$$

Here $Y_i$ is the observed catch in the $i$th period, $k$ is the number of vessels, $\epsilon$ is search parameter defined in section 2, and $t$ is the search time in the $i$th period. For simplicity, $t$ is set equal to 1 (although $t$ itself can be treated as a random variable (Mangel (1983)). In the simulation, the value $\epsilon = 0.01$ is used. To find the catch in period $l$, a random number, $X$, that is uniformly distributed on [0, 1] is drawn. The catch in period $l$, $Y_l$, is the integer that satisfies

$$(A.1)\quad \sum_{j=0}^{Y_l}\binom{N_0 - \sum_{i}^{l-1} Y_i}{j}(1-e^{-k\epsilon t})^j \times (e^{-k\epsilon t})^{N_0 - \sum_{i}^{l-1} Y_i - j} < X < \sum_{j=0}^{Y_l+1}\binom{N_0 - \sum_{i}^{l-1} Y_i}{j}(1-e^{-k\epsilon t})^j \times (e^{-k\epsilon t})^{N_0 - \sum_{i}^{l-1} Y_i - j}.$$

In the event that one of the inequalities is replaced by an equality, then $Y_l$ is modified accordingly.

# Relations Among Net Reproductive Rate and Life History Parameters for Lake Whitefish (*Coregonus clupeaformis*)

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Jensen, A. L. 1985. Relations among net reproductive rate and life history parameters for lake whitefish (*Coregonus clupeaformis*). Can. J. Fish. Aquat. Sci. 42: 164–168.

An equation is derived that relates net reproductive rate to six life history parameters; the equation is applied to determine changes in the net reproductive rate of lake whitefish (*Coregonus clupeaformis*) that result from variation in these life history parameters. Changes in age at maturity and survival of immature fish are the only parameters that have a large effect on the net reproductive rate. Age at maturity occurs near the inflection of the growth curve, and this implies a relationship between age at maturity, length at maturity, the growth coefficient, and asymptotic length.

Nous avons formulé une équation mettant en relation le taux de reproduction net d'un organisme avec six paramètres de son cycle biologique ; nous avons employé cette formule pour étudier les fluctuations du taux de reproduction net que provoquent les variations de ces paramètres chez le Grand corégone (*Coregonus clupeaformis*). L'âge à maturité et la survie des poissons immatures sont les seuls paramètres qui aient un effet important. L'âge à maturité se trouve près du point où la courbe de croissance s'infléchit, ce qui indique qu'il y a une relation entre l'âge et la longueur du poisson à maturité, le coefficient de croissance et la longueur asymptotique.

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Exploitation changes the life history parameters (growth, mortality, age of maturity, and fecundity) of fish populations (Ricker 1975; Beverton and Holt 1957), and to understand the possible effect of fishing on the ability of exploited populations to adapt to environmental change one should understand the effect of changes in life history parameters. Population genetic analyses have shown that populations with higher intrinsic rates of natural increase ($r$) dominate in competition (Fisher 1958; Roughgarden 1979), and therefore, life history studies have been concerned with the effect of changes in life history parameters on intrinsic rates of increase (Fisher 1958; Cole 1954; Roughgarden 1979). From an ecological viewpoint this approach may be limited because most species exist in saturated environments and abundance fluctuates in response to changes in the conditions of survival and growth resulting from changes in factors such as weather (Andrewartha and Birch 1954) and abundance of predators (Moller 1984). For most species an important ecological question is their capacity to respond to environmental perturbations. In my study of lake whitefish (*Coregonus clupeaformis*) I assume that populations fluctuate about an average carrying capacity with an average net reproductive rate of 1, and the life history parameters are evaluated not in terms of a maximization of $r$ but rather in terms of their potential for reproductive response when perturbations displace populations from equilibrium.

A distinctive feature of fishes is their wide variation in life history parameters; in different environments growth, age at maturity, size at maturity, fecundity, and mortality vary. This variation has both environmental and genetic components (Larkin 1978). There is much variation in life history parameters among different lake whitefish populations (Healey 1975; Jensen 1981). Total instantaneous mortality rates of mature fish range from 0.20 to 2.81, the proportion of females ranges from 0.37 to 0.86, eggs per kilogram of mature female biomass ranges from 15 800 to 34 300, growth coefficients range from 0.09 to 0.96, asymptotic weights range from 1.87 to 5.32 kg, and age at maturity ranges from 2 to 10 yr (Jensen 1981). I hypothesize that lake whitefish have evolved a flexibility that allows them to persist in different environments rather than optimum parameter values for a static environment. Variable growth, fecundity, and maturity may permit a rapid response to a changing environment.

## Model Development

To examine the potential importance of life history parameters in adapting to perturbations, one determines the effect of change in the life history parameters on the net reproductive rate $R_0$. Life history information is described in the equation for the net reproductive rate

$$(1) \quad R_0 = \int_0^{x_v} s(x)\,m(x)\,dx$$

where $s(x)$ is the proportion of eggs surviving to age $x$, $m(x)$ is the number of eggs produced by an individual of age $x$, and $x_v$ is the oldest age attainable. The life span was separated into two stages, a prematurity life stage and a mature life stage, and it was assumed that mortality was constant in each stage. Mortality

is not constant, but over an interval of time the effect of an average mortality and mortality that is a function of time are identical (Keyfitz 1977). Fecundity is assumed proportional to weight, and application of von Bertalanffy's equation gives

$$(2)\quad m(x) = HW_\infty\{1 - \exp[-K(x - x_0)]\}^3$$

where $H$ is the number of eggs produced per unit weight of mature fish, $W_\infty$ is the asymptotic weight, $K$ is a growth parameter, and $x_0$ is the theoretical age when size is zero.

Survival of the recruited members of a fish population is described by the exponential equation

$$(3)\quad s(x) = s(x_m)\exp[-Z_2(x - x_m)]$$

where $Z_2$ is the instantaneous total mortality coefficient of mature fish and $s(x_m)$ is the proportion that survive to maturity, age $x_m$. The proportion that survive to maturity also can be written as $s(x_m) = \exp(-Z_1 x_m)$. $Z_m$ is the average instantaneous mortality rate of all life stages prior to maturity. Substitution of equations (2) and (3) into the equation for the net reproductive rate $R_0$ gives

$$(4)\quad R_0 = \int_{x_m}^{x_v} HW_\infty\{1 - \exp[-K(x - x_0)]\}^3 \times \exp[-Z_1 x_m - Z_2(x - x_m)]dx$$

which upon integration gives

$$(5)\quad R_0 = HW_\infty \exp(-Z_1 x_m) \sum_{n=0}^{3} \frac{U_n \exp[-nK(x_m - x_0)]}{Z_2 + nK} \times \{1 - \exp[-Z + nK)(x_v - x_m)]\}$$

where $U_0 = 1$, $U_1 = -3$, $U_2 = 3$, and $U_3 = -1$. Equation (5) was applied to determine the relation near equilibrium between $R_0$ and the life history parameters $H$, $Z_1$, $Z_2$, $x_m$, $K$, and $W_\infty$. Equation (5) also could be applied to examine the relations among population parameters such as $K$ and $x_m$ with an $R_0$ of 1 but this would require numerical solution of the equation. A simple equation for the relation between $K$ and $x_m$ was developed from the growth equation.

## Methods

First, the potential for reproductive response of a lake whitefish population fluctuating about an equilibrium was examined as a function of its life history parameters, and then the relations among some of the parameters were examined. The effects of variation of parameters on the net reproductive rate can be determined directly because $R_0$ is an explicit function of the life history parameters; the parameters $R_0$ and $r$ are related by the equation $R_0 = e^{rT}$ where $T$ is generation time. The combinations of life history parameters consistent with observed parameters and that give an $R_0$ of 1 were found and then the effects of changes in parameters on the net reproductive rate were determined.

Equation (5) was applied to determine the changes in $R_0$ that could occur with changes in the population parameters over the observed values. Equation (5) was fitted to data for lake whitefish of Lake Michigan (Jensen 1981); the resulting parameter values are listed in Table 1. The estimate of the mortality coefficient for ages 0–4 was found by letting $R_0 = 1$ and solving for $Z_1$ in equation (5).

A distinctive feature of the life history of fishes is the high fecundity and low survival of young. To examine the significance of the impact of fecundity on the relations among $R_0$ and other life history parameters, I did calculations with the observed fecundity of 17 384 and with a fecundity of 1. For calculations done using a fecundity of 1 the first stage mortality was decreased to 0.50 and the second stage mortality was decreased to 0.2988; these values together with those of Table 1 for the remaining parameters give $R_0 = 1$.

TABLE 1. Estimates of parameter values for lake whitefish; when fecundity is 1 the mortality of first and second stages is decreased to the values in the parentheses.

| Parameter | Symbol | Value |
|---|---|---|
| Asymptotic weight (kg) | $W$ | 3.5 |
| Growth parameter | $K$ | 0.30 |
| Age at maturity | $x_m$ | 4 |
| Oldest age | $x_v$ | 25 |
| Eggs per unit female biomass | $H$ | 17 384 (1) |
| First stage mortality | $Z_1$ | 2.56 (0.50) |
| Second stage mortality | $Z_2$ | 1 (0.2989) |
| Theoretical age when length equals zero | $x_0$ | 0 |

## Results and Discussion

The life history parameters I examined were fecundity, the growth coefficient, mortality of adults, mortality of young life stages, and age at maturity. Change in the reproductive rate $R_0$ with change in fecundity is linear, and over the observed range of fecundity, if other parameters remain constant, $R_0$ varied from approximately 1 to 2 (Fig. 1). $R_0$ could vary from less than 0.5 to more than 2 (Fig. 2) over the range of observed growth rates, and the rate of increase in $R_0$ decreases for large growth coefficients because of the constraint of a fixed asymptotic size. The relation between $R_0$ and $K$ is affected little by fecundity (Fig. 2). $R_0$ decreases exponentially as adult mortality ($Z_2$) increases (Fig. 3) but $R_0$ changes little over a wide range of mortality.

$R_0$ is inversely related to age of maturity; fecundity effects the slope of this relation (Fig. 4). If maximization of $r$ is important, it is difficult to explain why delays in maturity are observed in natural populations given the effect of maturity on $R_0$. Stearns and Crandall (1981) reviewed several hypotheses that have been proposed to explain a delay in maturity. One explanation for a delay is selection at high population densities or $K$ selection but

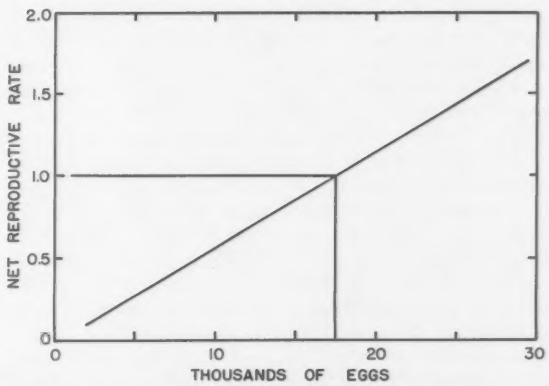


FIG. 1. Relation between net reproductive rate and thousands of eggs produced per kilogram of female lake whitefish.

TABLE 2. Growth parameters and age and length when all females are mature for nine different populations of lake whitefish.

| Location | $K$ | $L_\infty$ | Maturity age | Maturity length | Reference |
|---|---|---|---|---|---|
| Lake Opeongo | 0.11 | 540 | 7 | 286 | Kennedy 1943 |
| Cliff Lake | 0.18 | 440 | 9 | 354 | Fenderson 1964 |
| Great Slave Lake | 0.14 | 585 | 12 | 476 | Kennedy 1953 |
| Great Bear Lake | 0.09 | 735 | 9 | 419 | Kennedy 1949 |
| Lake Superior | 0.09 | 505 | 11 | 321 | Edsall 1960 |
| Lake Michigan | 0.42 | 615 | 5 | 557 | Brown 1968 |
| Lake Michigan | 0.31 | 685 | 5 | 535 | Brown 1968 |
| Lake Superior | 0.32 | 575 | 8 | 531 | Dryer 1964 |
| Green Bay | 0.31 | 665 | 4 | 473 | Mraz 1964 |

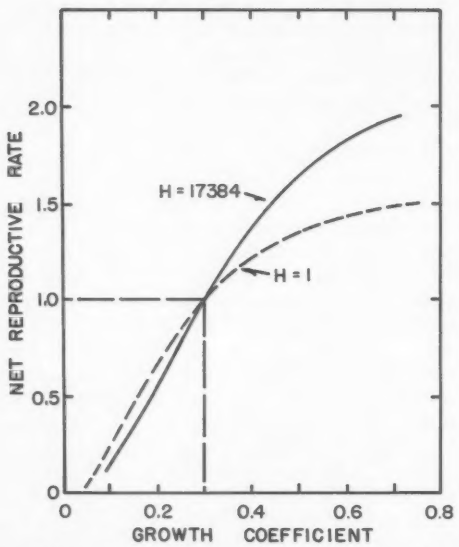


FIG. 2. Relation between net reproductive rate and growth coefficient for two different levels of fecundity for lake whitefish.

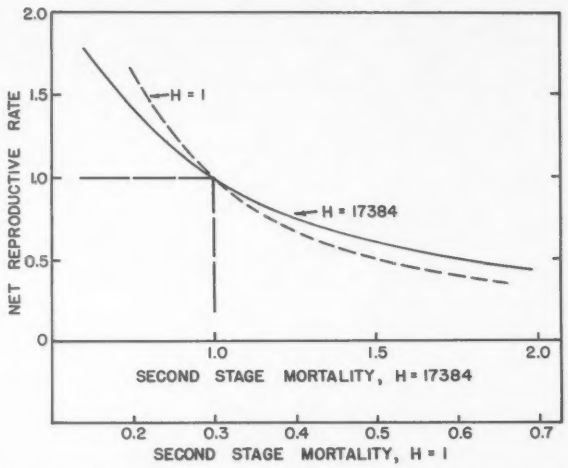


FIG. 3. Relation between net reproductive rate and second stage total instantaneous mortality coefficient for two different levels of fecundity for lake whitefish.

most fish would not fit the description of $K$-selected species. Another explanation proposed for the delay is that in a declining population the rate of decrease is a minimum when age at maturity is a maximum; but this is not true for fish because age at maturity tends to decrease for fish experiencing high fishing or natural mortality (Jensen 1981). These explanations do not describe the observed dynamics of fish populations and probably do not apply to other species (Stearns and Crandall 1981). More reasonable explanations are that a delay in maturity results in improved survival or increases fitness in the face of catastrophic larval mortality (Stearns and Crandall 1981).

The analysis of the effect of $x_m$ on $R_0$ indicates that maintenance of a potential for response to favorable conditions for survival and growth, which should increase fitness, could result in delayed maturity. Although $R_0$ increases greatly when $x_m$ decreases, if $x_m$ decreases to the lowest age physiologically possible, $R_0$ will eventually approach 1 through change in other parameters, and with a combination of life history parameters in which maturity occurs at the youngest possible age, a population would have little capacity to respond to change.

Change in survival of immature fish has a large impact on $R_0$ when fecundity is high as in lake whitefish and other fishes (Fig. 5) but it has little impact when fecundity is low. Increases in survival of larvae is assumed to be the major compensatory response of fish populations to exploitation (Beverton and Holt 1957, 1959; Ricker 1975). If change in mortality of larvae were dependent on density of adults, this would be a compensatory mechanism with a high potential for response to changing conditions of survival and growth; whether or not mortality of larvae is dependent on density of adults is still uncertain (Lasker and Sherman 1979; Van Winkle 1977) although Ware (1980) assumed that such a relation exists.

In analyses of life history parameters, one assumes that the parameters vary independently so that effects of each parameter can be identified (Stearns and Crandall 1981), but relations among life history parameters are complex and important in species with indeterminate growth such as lake whitefish. For lake whitefish a high mortality is associated with a high growth rate, a high growth rate is associated with a low age at maturity, and a high growth rate is associated with a low asymptotic weight (Jensen 1981).

A relation also occurs among the parameters $x_m$, $s(x_m)$, $K$, and $L_\infty$ because the inflection of the growth curve is at or slightly after maturity. When growth is described by the von Bertalanffy

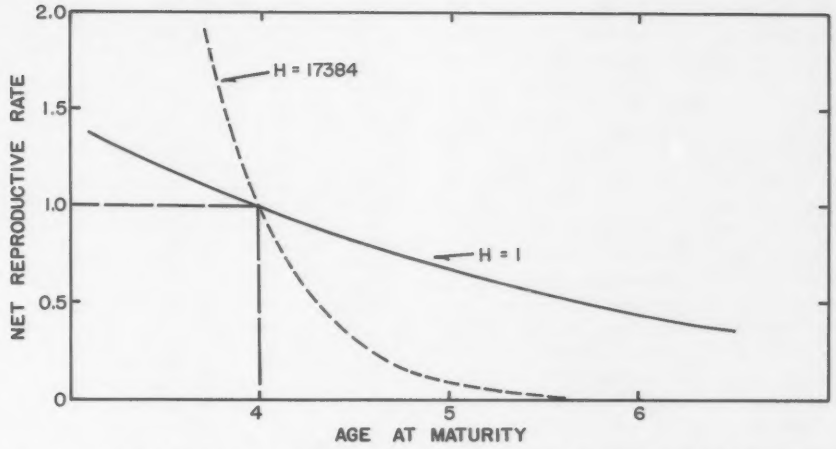


FIG. 4. Relation between net reproductive rate and age at maturity for two different levels of fecundity for lake whitefish.

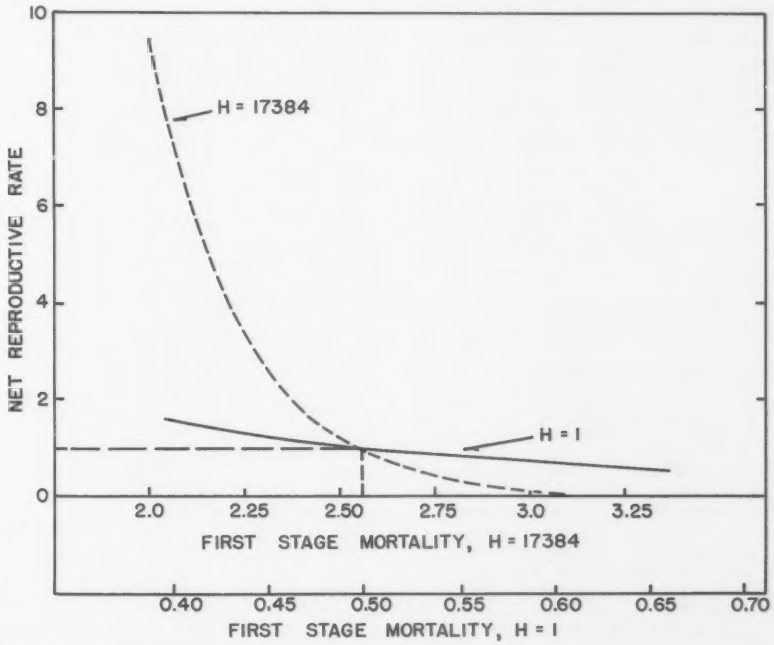


FIG. 5. Relation between net reproductive rate and first stage total instantaneous mortality coefficient for two different levels of fecundity for lake whitefish.

growth equation:

(6) $L(x) = L_\infty\{1 - \exp[-K(x - x_0)]\}$

(7) $W(x) = aL(x) = W_\infty\{1 - \exp[-K(x - x_0)]\}^b$

age at the inflection point of the growth in weight curve is related to the growth coefficient and asymptotic length (see Appendix) as

(8) $x_i - x_0 = \ln(b)/K$

(9) $L(x_i) = L_\infty(1 - 1/b)$

where $a$ and $b$ are parameters and $x_i$ is age at the inflection point. If $x_0 = 0$ and $b = 3$, then $x_i = 1.099\,(1/K)$ and $L(x_i) = 0.67L_\infty$. Applying least squares to relate age at maturity with $K$ and to relate length at maturity with $L_\infty$ for lake whitefish (Table 2) gives the equations $x_m = 1.11(1/K)$ and $L(x_m) = 0.74L_\infty$. Both regressions are significant ($P < 0.01$) and indicate that maturity occurs at or slightly after the inflection of the growth curve. These equations indicate that faster growing fish mature at an earlier age and attain smaller asymptotic sizes. Equations (8) and (9) could be applied to estimate age at maturity and asymptotic length.

Beverton and Holt (1959), Beverton (1963), and Holt (1962) investigated the association between length at maturity and

asymptotic length for many exploited marine fishes and found that $L(x)/L_\infty$ varied from 0.64 to about 0.76, which also indicates that $L(x)$ equals or is slightly greater than the size at the inflection point. Murphy (1968) assumed that variation in reproductive life span was associated with variation in predictability of reproductive success, but with additional data, Roff (1981) showed that the association found by Murphy (1968) was not significant and Roff (1981) concluded that variation in reproductive life span was associated with age at maturity. Pauly (1982) examined the relation among natural mortality, growth, and mean annual water temperature for 175 different populations of fish which included 84 different species and he found that, given the mean annual water temperature, the natural mortality coefficient could be predicted reliably from the growth parameters ($R^2 = 0.85$). The results of Pauly (1982) and Jensen (1981) together with those I presented for growth indicate that an increase in mortality is associated with an increased rate of growth and an earlier age and smaller size at maturity. A smaller size at maturity and lower growth after maturity result in a lower asymptotic size. Ware (1980, 1982) and Roff (1981) have reached similar conclusions using considerably different approaches.

In summary, data for lake whitefish are consistent with the hypothesis that they have evolved a life history with reproductive flexibility that enables survival under a range of conditions, the life history parameters are not independent, and the relations among the life history parameters provide a rapid reproductive response to changing conditions of growth and survival.

## References


ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, IL.

BEVERTON, R. J. H. 1963. Maturation, growth, and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 154: 44–67.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II Mar. Fish. G.B. Minist. Agric. Fish. Food 19.

1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics, p. 142–180. *In* G. E. W. Wolstenholme and M. O'Connor [ed.] The lifespans of animals. Ciba foundation colloquia on ageing. Vol. 5. Little, Brown and Company, Boston, MA.

BROWN, R. 1968. Whitefish in Lake Michigan. M.S. thesis. The University of Michigan, Ann Arbor, MI.

COLE, L. C. 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29: 103–137.

DRYER, W. R. 1964. Movements, growth, and rate of recapture of whitefish tagged in the Apostle Islands areas of Lake Superior. U.S. Fish Wildl. Serv. Fish. Bull. 63: 611–618.

EDSALL, T. A. 1960. Age and growth of the whitefish (*Coregonus clupeaformis*) of Munising Bay, Lake Superior. Trans. Am. Fish. Soc. 89: 323–332.

FENDERSON, O. C. 1964. Evidence of subpopulations of lake whitefish involving a dwarfed form. Trans. Am. Fish. Soc. 93: 77–94.

FISHER, R. A. 1958. The genetical theory of natural selection. 2nd revised ed. Dover Publications, New York, NY. (Original published in 1930)

HEALEY, M. C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. 32: 427–448.

HOLT, S. J. 1962. The application of comparative population studies to fisheries biology — an exploration, p. 51–69. *In* E. D. LeCren and M. W. Holdgate [ed.] The exploitation of natural animal populations. John Wiley & Sons, New York, NY.

JENSEN, A. L. 1981. Population regulation in lake whitefish, *Coregonus clupeaformis* (Mitchill). J. Fish Biol. 19: 557–573.

KENNEDY, W. A. 1943. The whitefish of Lake Opeongo, Algonquin Park, Ontario. Univ. Toronto Stud. Biol. Ser. 51 Vol. 62: 23–66.

1949. Some observations on the caregonine fish of Great Bear Lake, Northwest Territories. Bull. Fish. Res. Board Can. 82: 1–10.

1953. Growth, maturity, fecundity and mortality in the relatively unexploited whitefish, *Coregonus clupeaformis*, of Great Slave Lake. J. Fish. Res. Board Can. 10: 413–441.

KEYFITZ, N. 1977. Applied mathematical demography. John Wiley & Sons, New York, NY.

LARKIN, P. A. 1978. Fisheries management — an essay for ecologists. Annu. Rev. Ecol. Syst. 9: 57–73.

LASKER, R., AND K. SHERMAN. 1979. The early life history of fish: recent studies. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178.

MOLLER, H. 1984. Reduction of a larval herring population by jellyfish predator. Science (Wash., DC) 224: 621–622.

MRAZ, D. 1964. Age, growth, sex ratio, and maturity of the whitefish in central Green Bay and adjacent waters of Lake Michigan. U.S. Fish Wildl. Serv. Fish. Bull. 63: 619–634.

MURPHY, G. I. 1968. Pattern in life history and the environment. Am. Nat. 102: 391–403.

PAULY, D. 1982. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Cons. Int. Explor. Mer 39: 175–192.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191.

ROFF, D. A. 1981. Reproductive uncertainty and the evolution of iteroparity: why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. 38: 968–977.

ROUGHGARDEN, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. Macmillan, New York, NY.

STEARNS, S. C., AND R. E. CRANDALL. 1981. Quantitative predictions of delayed maturity. Evolution 35: 455–463.

VAN WINKLE, W. [ED.] 1977. Proceedings of the conference on assessing the effects of power-plant-induced mortality on fish populations. Oak Ridge National Laboratory, Oak Ridge, TN.

WARE, D. M. 1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37: 1012–1024.

1982. Power and evolutionary fitness of teleosts. Can. J. Fish. Aquat. Sci. 39: 3–13.


## Appendix

The relation between age at the inflection point and the growth parameters is obtained below. The von Bertalanffy growth equation is

$$W(x) = W_\infty[1 - e^{-K(x-x_0)}]^b$$

and the inflection point of this growth curve occurs where the second derivative equals zero. From the above equation

$$dW/dx = bKW_\infty e^{-K(x-x_0)}[1 - e^{-K(x-x_0)}]^{b-1}$$

and

$$d^2W/dt^2 = b(b-1)K^2W_\infty e^{2K(x-x_0)}[1 - e^{-K(x-x_0)}]^{b-2} - bK^2W_\infty e^{-K(x-x_0)}[1 - e^{-K(x-x_0)}]^{b-1}.$$

Setting the second derivative to zero and dividing through by $bK^2W_\infty e^{-K(x-x_0)}$ gives

$$(b-1)e^{K(x-x_0)}[1 - e^{-K(x-x_0)}]^{b-2} - [1 - e^{-K(x-x_0)}]^{b-1} = 0.$$

Dividing both sides of the above equation by $[1 - e^{-K(x-x_0)}]^{b-2}$ gives

$$(b-1)e^{-K(x-x_0)} - [1 - e^{-K(x-x_0)}] = 0$$

and solution of the above equation for $(x - x_0)$ gives equation (8). Equation (9) is obtained from the equation for growth in length:

$$L(x) = L_\infty[1 - e^{-K(x-x_0)}].$$

In equation (8), when $x = x_i$, $K(x_i - x_0) = \ln(b)$, which gives $-K(x_i - x_0) = -\ln(b) = \ln(1/b)$, and hence

$$e^{-K(x_i-x_0)} = 1/b$$

and substitution into the above growth equation gives equation (9).

# Ségrégation édaphique et bathymétrique chez le crabe des neiges, *Chionoecetes opilio* (O. Fabr.), dans le sud-ouest du golfe du Saint-Laurent[1]

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Coulombe, F., J.-C. F. Brêthes, R. Bouchard et G. Desrosiers. 1985. Ségrégation édaphique et bathymétrique chez le crabe des neiges, *Chionoecetes opilio* (O. Fabr.), dans le sud-ouest du golfe du Saint-Laurent. Can. J. Fish. Aquat. Sci. 42: 169–180.

Des observations sur une population de *Chionoecetes opilio* ont été effectuées au cours des été 1980 et 1981 dans le sud-ouest du golfe du Saint-Laurent, à l'entrée de la baie des Chaleurs et de la baie de Gaspé. L'échantillonnage a été réalisé à l'aide d'un chalut à perche et de casiers appâtés, à des profondeurs variant de 45 à 125 m. Les largeurs de carapace des crabes des deux sexes ont été mesurées et la maturité physiologique déterminée par indice biométrique. Les individus prématures des deux sexes se distribuent préférentiellement aux niveaux bathymétriques supérieurs sur des substrats hétérogènes gravelovaseux tandis que les adultes sont rencontrés surtout en profondeur sur les fonds de vase et de vase sableuse. On émet l'hypothèse que les jeunes crabes descendent vers les fonds de vase où se produit le recrutement à la pêche. Ce déplacement serait concomitant à l'apparition de la maturité physiologique.

A population of *Chionoecetes opilio* was studied during the summers of 1980 and 1981 in the southwestern Gulf of St. Lawrence, at the entrance of the Bay of Chaleur, and the Gaspé Bay. Sampling was conducted with beam trawls and baited traps at depths ranging from 45 to 125 m. Crab shell width of both sexes was measured and physiological maturity determined according to a biometrical index. Immature individuals of both sexes are essentially localized on the upper bathymetrical levels, on gravelly mud, whereas adults are found mainly on mud or sandy mud bottoms. We hypothesize that young crabs move down to the muddy bottom where recruitment to the fishery occurs. This deplacement seems to be concomitant with physiological maturity.

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L'espèce *Chionoecetes opilio* (O. Fabr.) est commune dans le golfe du Saint-Laurent où elle est exploitée commercialement. L'habitat habituel du crabe des neiges correspond aux vasières profondes (Brunel 1960) mais il peut être également rencontré sur des fonds plus durs (Powles 1968). Des travaux parallèles de Ledoyer (1975) et Miller (1975), effectués à l'entrée de la baie des Chaleurs et de la baie de Gaspé, ont montré que des concentrations de petits crabes étaient observées à faible profondeur sur des fonds graveleux ou rocheux. Par la suite, au cours de pêches exploratoires effectuées avec des engins commerciaux, Miller et O'Keefe (1981) observent une augmentation de la taille des individus avec la profondeur dans la baie Conception à Terre-Neuve.

L'hypothèse est donc que les différentes composantes de la population de crabe des neiges (mâles, femelles, matures, immatures) ne sont pas distribués au hasard dans un seul habitat mais qu'il devrait exister une certaine ségrégation liés à des facteurs écologiques, tels la bathymétrie et la nature granulométrique du sédiment. Le but de ce travail, réalisé au cours des étés 1980 et 1981, dans le sud-ouest du golfe du Saint-Laurent, est de vérifier la répartition bathymétrique de l'espèce *C. opilio* et d'évaluer l'influence de la nature du substrat sur cette répartition.

## Description de l'aire d'étude

La zone prospectée se situe dans le sud-ouest du golfe du Saint-Laurent, entre 64°00′ et 64°30′ O et entre 48°10′ et 48°50′ N. Elle comprend l'entrée de la baie des Chaleurs, la Malbaie et l'entrée de la baie de Gaspé (fig. 1), soit une étendue d'environ 2500 km$^2$. La sédimentologie du secteur a été étudiée par Brunel (1970), Loring et Nota (1973), Ledoyer (1975) et Coulombe (1983). On peut y définir quatre zones sédimentologiques (fig. 2) : les vases pures, les vases sableuses, les sables vaseux et les graviers pélitiques.

La zone des vases pures est disposée essentiellement dans l'axe de la baie des Chaleurs à des profondeurs généralement supérieures à 90 m. La teneur en matériel pelitique de ces sédiments est rarement inférieure à 95 %, la fraction restante étant du sable très fin. On les retrouve également dans la baie de Gaspé au-delà de l'isobathe de 75 m.

La zone des vases sableuses occupe une surface plus restreinte que la précédente. Elle forme une zone de transition entre les vases pures et les sables vaseux de part et d'autre du

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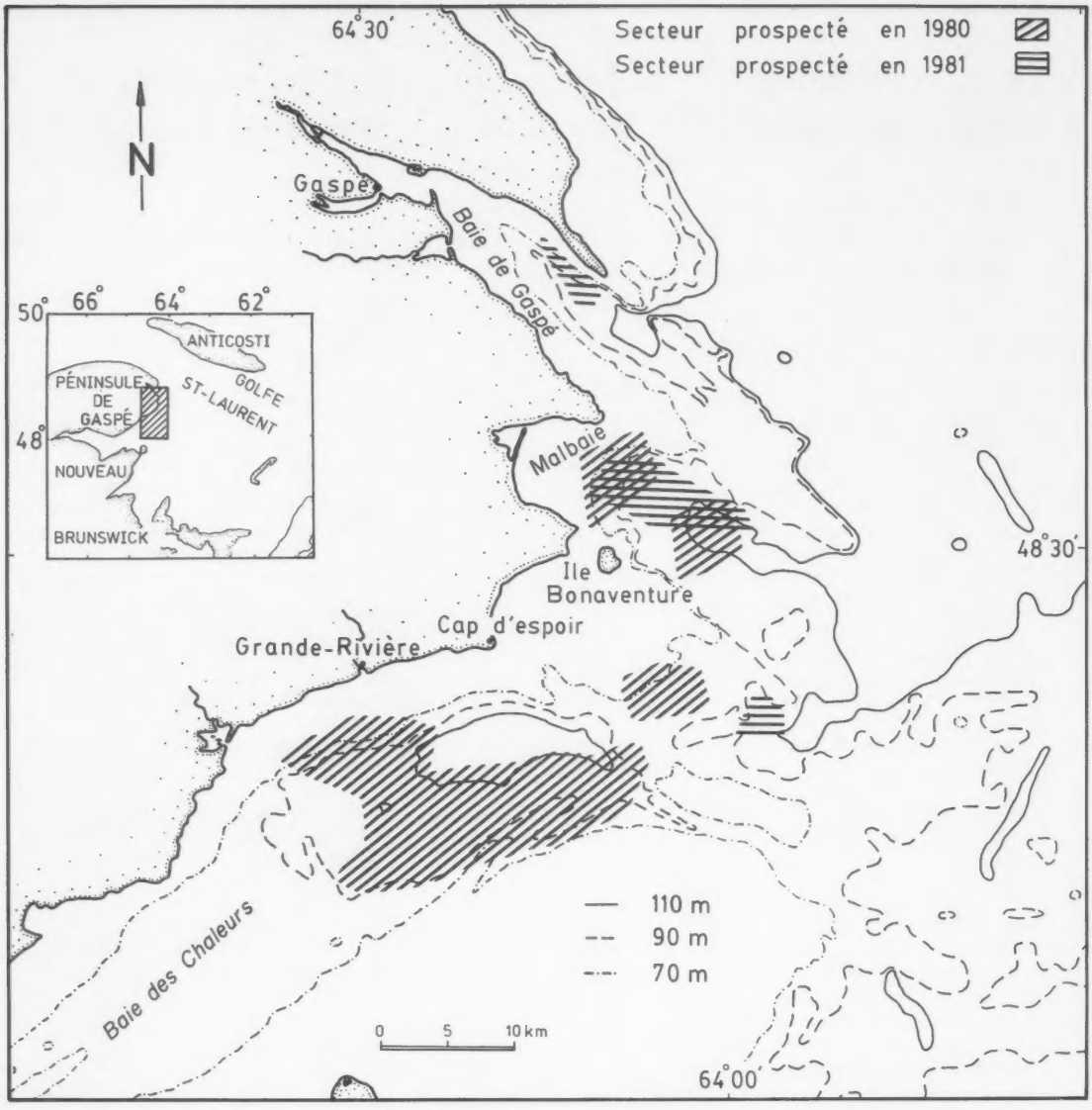


FIG. 1. Localisation du site d'étude.

chenal de la baie des Chaleurs. Sa profondeur varie alors entre 75 et 90 m. Elle s'étend face à la Malbaie où elle se juxtapose aux sables vaseux. Elle s'installe à des profondeurs comprises entre 70 et 120 m. On se rappellera que les vases pures occupaient de telles profondeurs dans la baie des Chaleurs. Les pélites contribuent pour 60 à 80 % du contenu des échantillons. Les vases sableuses entourent la zone des vases dans la baie de Gaspé.

Les sables vaseux sont, avec les vases pures, l'une des deux zones importantes en superficie dans le secteur étudié. Cette zone se situe essentiellement autour des zones envasées de la baie des Chaleurs ainsi qu'à l'entrée de la Malbaie. Elle couvre une gamme de profondeurs comprises entre 35 et 75 m. La teneur relative de ses constituants est variable et fortement influencée par la proximité des autres zones sédimentaires.

Enfin, la zone des graviers pélitiques se localise de façon éparse dans le secteur, soit d'ouest en est : le long de la côte gaspésienne, face au Cap d'Espoir, dans l'axe nord-sud de l'Ile Bonaventure, au centre de la Malbaie. Enfin, une dernière plaque donne sur la mer ouverte au sud-est de l'Ile Bonaventure. Elle s'étend généralement de 20 à 35 m quoique sous certaines conditions elle puisse descendre jusqu'à 75 m. Elle se caractérise par la prépondérance de graviers et galets colmatés par des éléments plus fins.

Les études hydrologiques de Lauzier et al. (1957) et Lauzier et Bailey (1957) ont montré qu'aux environs de l'isobathe des 30 m, tendait à s'établir une thermocline entre les eaux superficielles, à fortes fluctuations thermiques et une couche intermédiaire dont les températures varient peu annuellement (−1 à 2°C). La couche d'eau profonde rencontrée entre 200 et

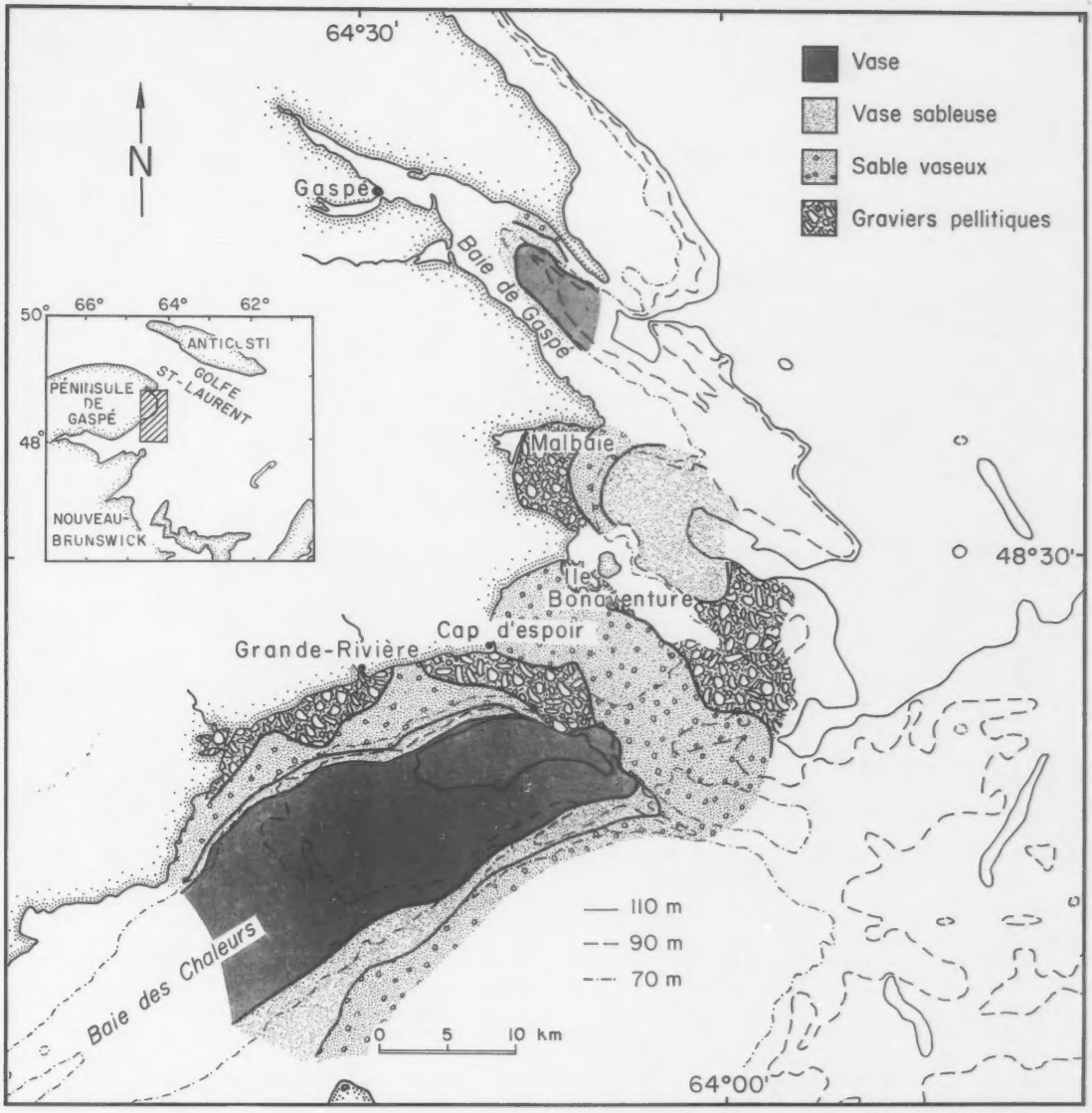


FIG. 2. Répartition des principaux types de substrat.

300 m dans le golfe du Saint-Laurent est absente puisque la profondeur maximale du chenal de la baie des Chaleurs est de 180 m (Loring et Nota 1973). On distingue donc selon Brunel (1970) : les eaux de surface de température variable et peu salées (25–31 ‰) et les eaux intermédiaires, très froides, de température moyenne avoisinant 0°C et de salinité plus élevée (31 à 33 ‰).

Faisant suite aux travaux de Brunel (1970), Ledoyer (1975) et Bellan (1978), l'étude de la structure des populations d'invertébrés benthiques a été complétée par Coulombe (1983). Un peuplement est associé aux fonds les plus envasés et correspond à celui des vases sous eaux arctiques (Ledoyer 1975) ou encore communauté arctique des vases cohésives (Brunel 1970) et qui est assimilable à la communauté du polychète *Maldane sarsi* et de l'ophiure *Ophiura sarsi* (Coulombe 1983). Les fonds hétérogènes qui nous intéressent (sables vaseux et graviers pélitiques) sont occupés par le peuplement des sables vaseux sous eaux arctiques (Ledoyer 1975) ou communauté subarctique des sables vaseux (Brunel 1970) et référable à la communauté du bivalve *Macoma calcarea* (Coulombe 1983). Le crabe des neiges, *C. opilio*, appartient à la fois à ces deux communautés, bien qu'il ait été plutôt considéré comme rattaché à la communauté des vases (Brunel 1970).

## Matériel et méthodes

L'échantillonnage a été réalisé en mai et septembre 1980 à l'entrée de la baie des Chaleurs et dans la Malbaie ; en 1981, le secteur de la Malbaie a été visité en mai, juillet et septembre et la baie de Gaspé en mai. Les profondeurs ont varié de 45 à 125 m.

TABLE 1. Résumé de l'échantillonnage effectué en 1980 et 1981 pour le crabe des neiges *C. opilio*. Substrat : HE = fonds hétérogènes envasés ; VS = vase sableuse ; V = vase. Engin : CH = chalut ; CA = casier appâté.

| Date | Lieu | Profondeur (m) | Substrat | Engin | Nombre de traits ou de levées |
|---|---|---|---|---|---|
| Mai 1980 | Malbaie | 80–90 | HE | CH | 4 |
| | | 90 | HE | CH | 3 |
| | | 100 | VS | CH | 2 |
| | | 110 | VS | CH | 7 |
| | Baie des Chaleurs | 75 | HE | CH + CA | 2 + 2 |
| | | 80–90 | HE | CH | 1 |
| | | 80–90 | VS | CH | 1 |
| | | 90–100 | VS | CH | 4 |
| | | 90–100 | V | CH | 1 |
| | | 100+ | VS | CH | 1 |
| | | 110+ | V | CH | 4 |
| Sept. 1980 | Malbaie | 80–90 | HE | CA | 3 |
| | | 90–100 | HE | CA | 2 |
| | | 100–110 | VS | CA | 5 |
| | Baie des Chaleurs | 110+ | V | CA | 3 |
| Mai 1981 | Gaspé | 70 | VS | CA | 12 |
| | | 80–90 | VS | CA | 12 |
| | | 90–100 | V | CA | 24 |
| | | 125 | V | CA | 12 |
| | | 80–90 | HE | CA | 24 |
| | | 90–100 | VS | CA | 12 |
| Juil. 1981 | Malbaie | 40–70 | HE | CA | 24 |
| | | 80–90 | HE | CA | 12 |
| | | 100 | VS | CA | 12 |
| Sept. 1981 | Malbaie | 60 | HE | CA | 12 |
| | | 75 | HE | CA | 12 |
| | | 90 | HE | CA | 12 |
| | | 110 | HE | CA | 12 |

Les crabes ont été pêchés par deux techniques différentes. En mai 1980, la baie des Chaleurs et la Malbaie ont été prospectées par 51 traits de chalut, d'une durée de 30 min chacun, et effectués entre le coucher et le lever du soleil. L'engin était un petit chalut à perche de 1,80 m d'ouverture horizontale équipé d'une poche dont la maille étirée est de 25 mm. Par la suite on a utilisé des casiers coniques, de type japonais, recouverts d'un maillage étiré de 45 mm et disposé en filières. En 1981, on a également employé des casiers aplatis afin d'augmenter la probabilité de capture des petits crabes. Aucune différence significative n'ayant été observée entre les captures des deux types de casiers (R. Bouchard, données non publiées) elles ont été considérées de la même façon. Les casiers étaient appâtés avec environ 1,5 kg de hareng congelé et laissés en place pour une période de l'ordre de 24 h. L'ensemble de l'échantillonnage est résumé au tableau 1.

La taille des crabes correspond à la largeur maximale de la carapace, mesurée au millimètre près. La maturité physiologique a été estimée par mesure biométrique : largeur de la pince pour les mâles et largeur du 5e segment abdominal pour les femelles. Cette méthode présente l'avantage d'être très rapide et non destructrice. Selon les données de Watson (1970), on a considéré comme mature un mâle dont le rapport de la largeur de la pince à la largeur de la carapace était égal ou supérieur à 0,19 et une femelle dont le rapport de la largeur de l'abdomen à la largeur de la carapace était égal ou supérieur à 0,55.

Pour éprouver la validité de la méthode utilisée, on a porté sur un graphique la largeur de la pince des mâles en fonction de la largeur de la carapace (fig. 3) : on peut identifier deux nuages, plus ou moins bien séparés par la droite $Lp = 0{,}19Lc$. On a également comparé la courbe d'apparition de la maturité obtenue par mesure biométrique (fig. 4) à celle obtenue par Watson (1970) à partir d'observation sur les tractus génitaux. Selon la méthode biométrique, 50 % des mâles sont matures à 62 mm de largeur de carapace, à comparer à la taille de 57 mm obtenue par Watson. Pour les femelles, le seuil est identique, 50 mm. La méthode biométrique semble surestimer la proportion des mâles immatures dans la population mais la précision semble suffisante pour le but poursuivi dans cette étude.

Le gradient bathymétrique a été divisé en cinq niveaux de profondeurs, moins de 80 m, de 80 m à moins de 90 m, de 90 m à moins de 100 m, de 100 m à moins de 110 m, 110 m et plus. De même on a retenu trois catégories de substrat : vases, vases sableuses et fonds hétérogènes envasés, qui regroupent les sables vaseux et les graviers pélitiques. On a comparé la répartition des immatures selon ces paramètres au moyen de tests non paramétriques, soient le test $u$ de Mann–Whitney et le test $K$ de Kruskal–Wallis. L'influence des deux paramètres

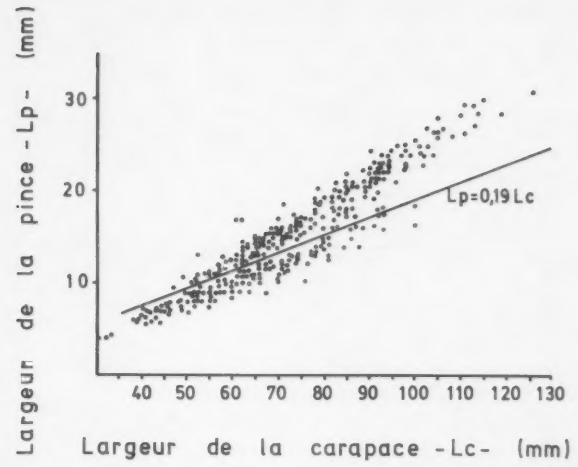


FIG. 3. Relation entre la largeur de la pince et la largeur de la carapace pour les mâles de *C. opilio*.

écologiques sur les distributions de fréquence de taille a été étudiée par l'analyse factorielle des correspondances (Benzecri et al. 1980). Cette technique est applicable aux tableaux de contingence et, plus généralement, aux tableaux de données formés de nombres entiers, positifs ou nuls.

L'analyse cherche la "meilleure" représentation simultanée des points observations et des points variables dans un système commun d'axes orthogonaux. La distance entre deux observations, respectivement deux variables, est donnée par la métrique du Khi-carré. L'interprétation est fondée, ici, sur l'étude de la projection plane des nuages des observations et des variables. Ces variables sont les largeurs de carapace, groupées en classes de 5 mm, exprimées en parties pour mille. Le pourcentage d'immatures a été introduit en variable supplémentaire, cette donnée n'intervient donc pas dans l'image générale de la projection mais sa position permet de préciser l'interprétation. Les observations ne correspondent pas, ici, aux prélèvements mais aux huit variables écologiques (cinq niveaux bathymétriques et trois substrats) pour les cinq périodes d'échantillonnage. Une donnée de la matrice correspond donc à la proportion d'individus d'une taille donnée sur un type de substrat, ou un niveau de profondeur, à une période donnée. Le programme informatique utilisé est celui décrit par Lebart et Fénelon (1975).

## Résultats

### Distribution des mâles

Les distributions de fréquence de taille (fig. 5 et 6) se répartissent autour d'un mode à 65–70 mm présent dans tous les prélèvements, quelles que soient la période, la région ou la profondeur. Sur les fonds de moins de 90 m, les distributions sont décalées vers les petites tailles où l'on peut noter un mode secondaire à 45 ou 50 mm. Dans les zones plus profondes, supérieures à 90 m, ce sont les grandes tailles qui dominent et le mode secondaire se situe vers 85–90 mm de largeur de carapace. Ce schéma est cohérent d'une région à l'autre et d'une période à l'autre. Le mode à 45 mm n'apparaît toutefois qu'en 1980 (fig. 5) et en mai 1981 dans la Malbaie (fig. 6A). Une exception paraît être la série de prélèvements effectués en juillet

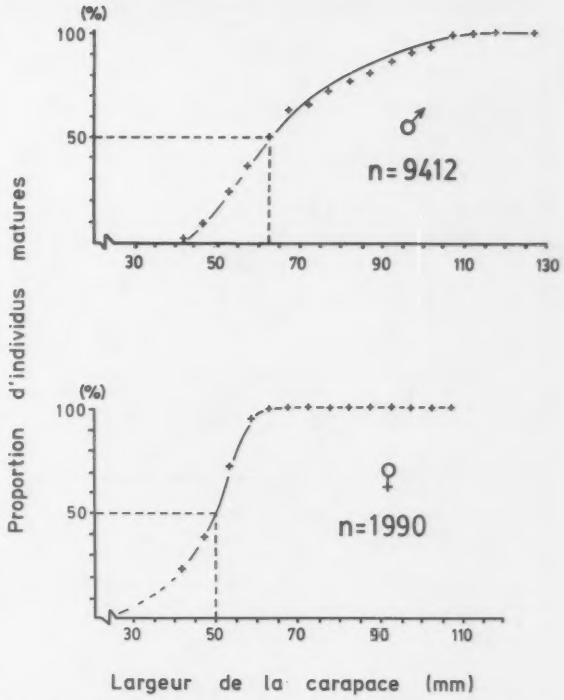


FIG. 4. Courbes d'apparition de la maturité physiologique obtenues par l'indice biométrique.

1981 (fig. 6C) où peu de différences ne sont observées entre les deux niveaux de profondeurs représentées.

Si l'on considère le pourcentage de mâles immatures dans les prélèvements, il diminue avec l'augmentation de la profondeur, d'une part, et avec l'augmentation de la fraction fine du sédiment d'autre part (fig. 7). Selon la bathymétrie, les fonds de moins de 80 m supportent, en moyenne, 61 % (±21 %) d'immatures, ceux de 80 à 90 m 65 % (±18 %), ceux de 90 à 100 m 46 % (±17 %), ceux de 100 à 110 m 29 % (±13 %) et les plus grandes profondeurs 12 % (±13 %). Selon la nature granulométrique du substrat, les fonds hétérogènes envasés en abritent 65 % (±11 %), les vases sableuses 22 % (±8 %) et les vases pures 36 % (±16 %). Une analyse de variance de rangs de Kruskal–Wallis effectuée sur les prélèvements provenant des fonds hétérogènes montre que la bathymétrie ne joue pas de rôle significatif lorsque les immatures se localisent sur ce type de substrat ($K = 0{,}2$ ; $K_{(2-0{,}05)} = 6{,}0$). Sur les fonds de vase sableuse, par contre, il y a une diminution significative de la proportion des juvéniles lorsque la profondeur augmente ($K = 12{,}8$ ; $K_{(2-0{,}01)} = 9{,}2$). Si l'on considère l'ensemble des profondeurs où l'on peut trouver soit des fonds hétérogènes, soit des vases sableuses, moins de 100 m, le test $U$ de Mann–Whitney indique, qu'en moyenne, les immatures sont mieux représentés sur le premier type de substrat, 65 %, que sur le deuxième, 40 % ($U = 38$ ; $U_{0,05} = 38$). Enfin, il n'y a pas de différence significative entre les vases et les vases sableuses pour les profondeurs supérieures ou égales à 100 m.

Pour interpréter l'analyse des correspondances, on a représenté, dans le plan factoriel formé par les deux premiers axes, la projection des classes de taille, d'une part, et celle de la position moyenne de chaque variable écologique, d'autre part (fig. 8).

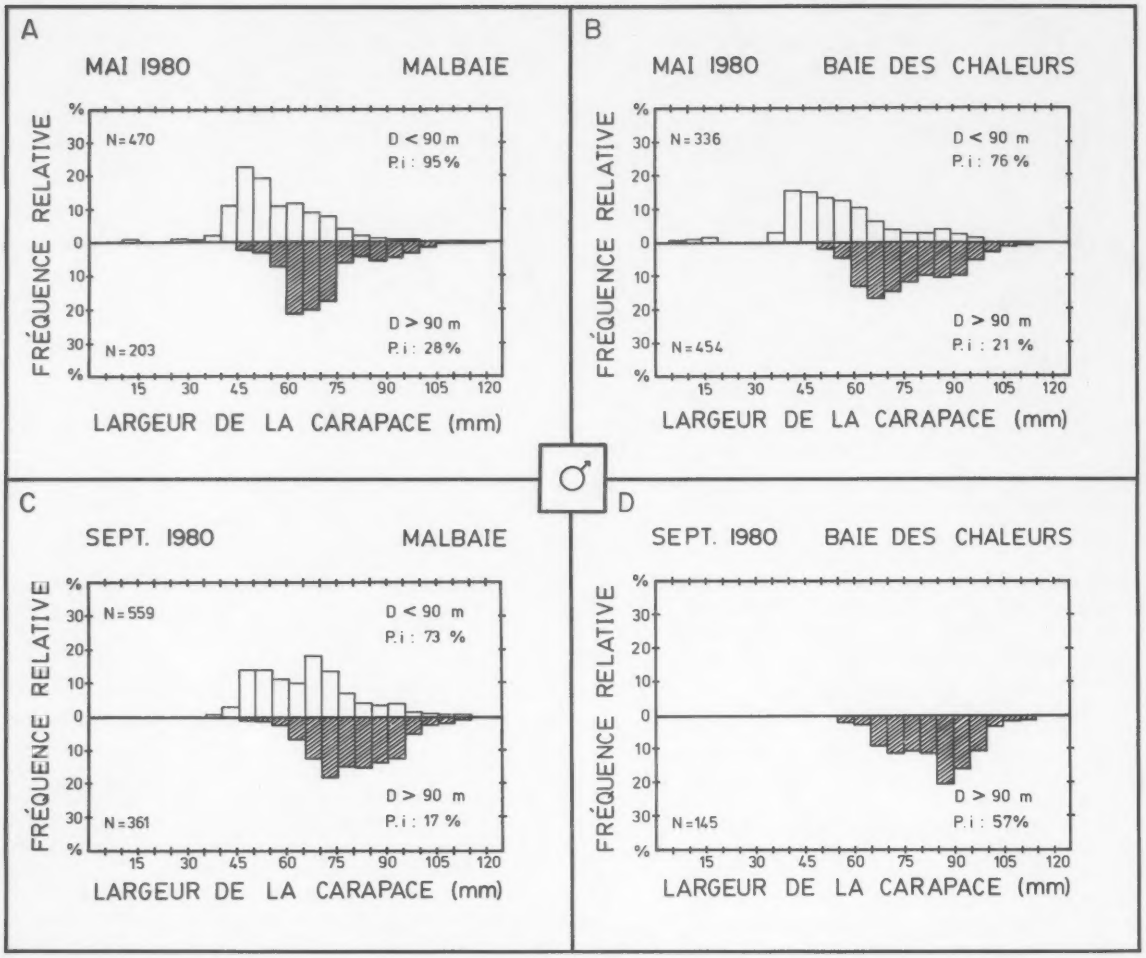


FIG. 5. Distribution des fréquences de taille de mâles de *C. opilio* récoltés en 1980 (*D* = profondeur ; *Pi* = pourcentage d'immatures ; *N* = nombre d'individus).

On note un étirement très net le long de l'axe 1 qui explique, à lui seul, 71 % de la variabilité des données, contre 10 % à l'axe 2 ; ceci traduit la corrélation assez marquée entre la granulométrie et la bathymétrie et aussi entre les classes de taille et les variables écologiques. Il y a ainsi une ségrégation de tailles liée à la nature du substrat et à la profondeur. En abscisse négative se localisent les plus petites classes de taille (55 mm et moins) associées aux profondeurs de moins de 90 m et aux substrats hétérogènes. La variable supplémentaire, soit le pourcentage d'immatures, apparaît reliée à cet ensemble. Il est opposé, sur le premier axe, aux plus grandes classes de taille (80 mm et plus) associées aux substrats plus fins et aux grandes profondeurs, 100 et 110 m. La strate de 90 m se situe en transition à proximité de l'origine des axes ; la classe de taille de 60 mm se retrouve dans la même situation pour l'ensemble des largeurs de carapace.

La variation temporelle de cette image est donnée par la projection sur le premier axe des variables écologiques pour chacune des périodes d'échantillonnage (fig. 9). Le schéma moyen de la fig. 8 n'apparaît pas constant dans le temps. La ségrégation selon la bathymétrie et le substrat apparaît nettement en mai 1980 et septembre 1980, même si les engins de capture sont différents. Elle subsiste encore en mai 1981. A cette époque, le rapprochement des faibles profondeurs avec la granulométrie plus fine est dû aux prélèvements effectués dans la baie de Gaspé. La ségrégation s'estompe en juillet et septembre 1981 avec une plus grande homogénéité de la population entre les différentes profondeurs et substrats.

## Distribution des femelles

La localisation des femelles paraît décalée par rapport à celle des mâles. Leur abondance est plutôt faible aux niveaux les plus élevés tandis qu'elles sont particulièrement bien représentées aux niveaux les plus profonds. Ceci pourrait toutefois être un biais introduit par la pêche au casier car les traits de chalut effectués en mai 1980 ont rapporté des quantités significatives de crabes femelles sur des fonds de 85 m. Le maillage des casiers utilisés paraît tronquer exagérément la distribution de fréquence de taille du côté des plus petits individus, inférieurs à 45 mm. Ces prélèvements reflètent donc une image déformée de

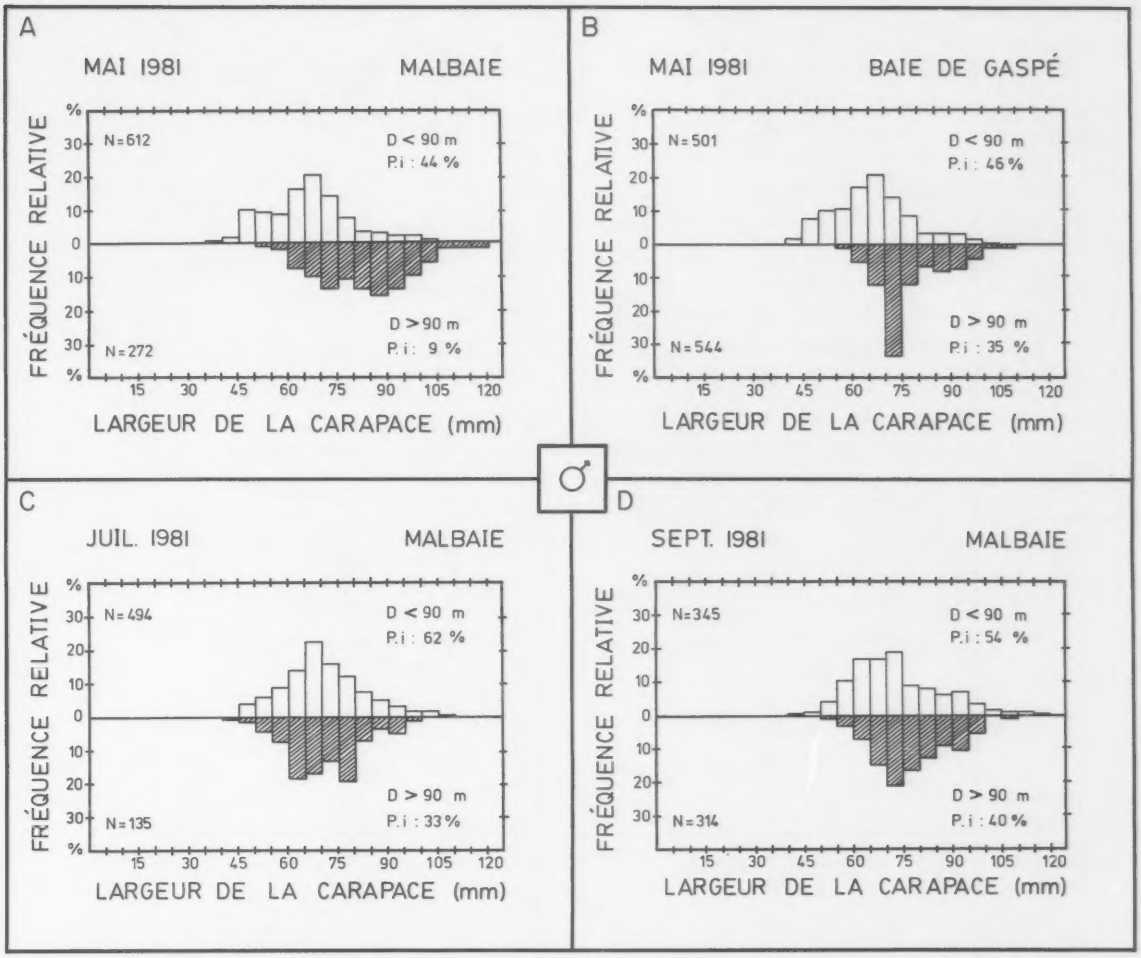


FIG. 6. Distribution des fréquences de taille des mâles de *C. opilio* récoltés en 1981 (même légende que pour la fig. 5).

la répartition des tailles des femelles dans le milieu. Une idée de cette répartition peut néanmoins être donnée par les prélèvements réalisés en 1980 (fig. 10). Comme pour les mâles, on observe une certaine augmentation de la taille avec la profondeur, un mode à 45–50 mm étant noté sur les fonds de moins de 90 m alors qu'un deuxième, autour de 65 mm, apparaît sur les grands fonds. La distribution des femelles immatures suit également ce schéma, du moins en 1980; on note 21 % de femelles immatures sur les fonds de moins de 90 m dans la Malbaie en mai (fig. 10A) et 60 % dans la baie des Chaleurs à la même période et aux mêmes profondeurs (fig. 10B). En septembre de la même année, on remarque encore 66 % de femelles immatures sur les fonds de moins de 90 m de la Malbaie (fig. 10D) bien que ces prélèvements aient été effectués au casier. En 1981, la proportion d'immatures pêchés reste constamment autour de 10 %.

### Rapport des sexes

Les rapports moyens des sexes, en terme de pourcentages de mâles observés dans les échantillons (fig. 11) montrent une tendance à l'augmentation de la proportion des femelles avec la profondeur. Au mois de mai, tant en 1980 qu'en 1981, cette proportion varie beaucoup d'un prélèvement à l'autre, ce qui pourrait indiquer une distribution en nuages composés soit de mâles soit de femelles. Ce rapport des sexes montre une variation saisonnière. Si les femelles adultes apparaissent assez bien représentées à toutes les profondeurs en début de saison, on ne les retrouve pratiquement plus qu'en profondeur à l'automne.

## Discussion

### Ségrégation bathymétrique et édaphique

Le déplacement des Crustacés Décapodes selon un gradient bathymétrique en fonction de leur taille est une observation courante. Elle a été faite, par exemple, pour le crabe *Cancer pagurus* en Manche (Brown et Bennett 1980), pour les langoustes de la famille des Palinuridae (Kanciruk 1980) et pour le homard européen, *Homarus gammarus*, bien que chez cette espèce la nature du substrat intervienne pour séparer adultes et juvéniles à un même niveau bathymétrique (Howard

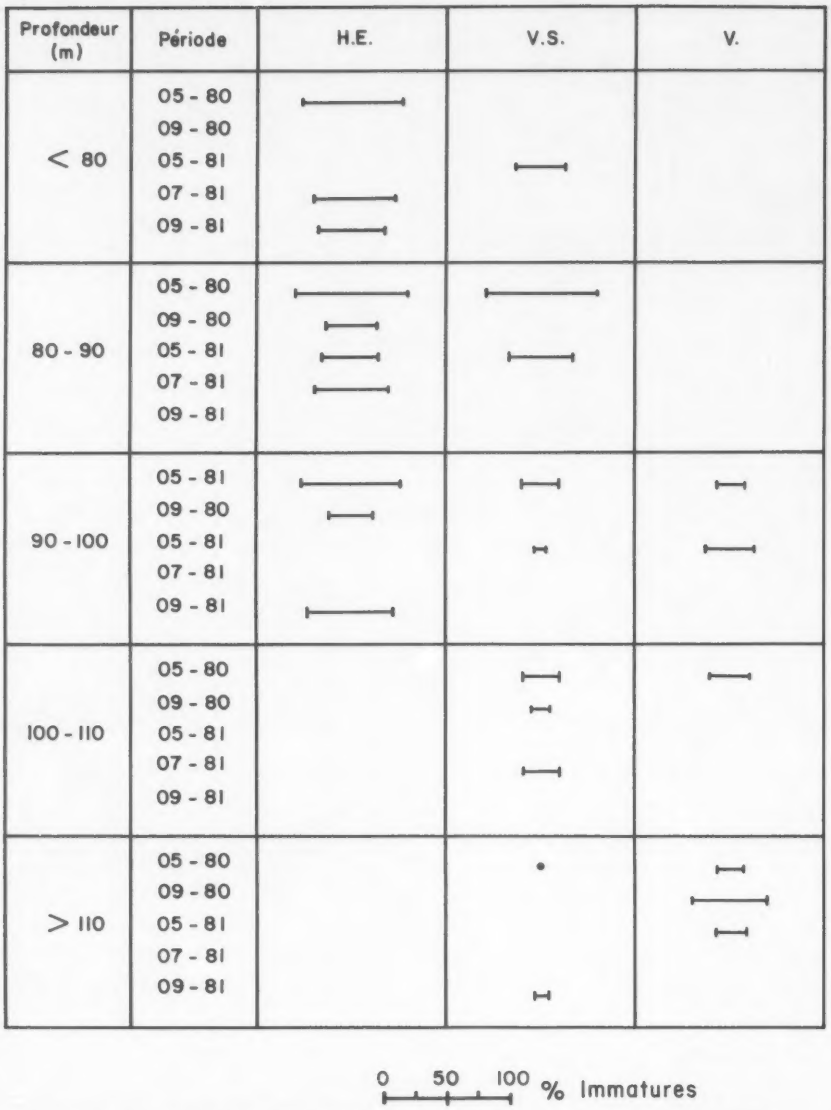


FIG. 7. Pourcentage de mâles immatures selon la bathymétrique et le substrat, toutes régions regroupées (HE = substrat hétérogène envasé ; VS = vase sableuse ; V = vase).

1980). Chez une espèce nettement vasicole comme la langoustine, *Nephrops norvegicus*, la profondeur ne joue aucun rôle (Chapman 1980). Chez *C. opilio*, l'augmentation de la taille avec la profondeur avait déjà été notée par Miller et O'Keefe (1981) dans la baie Conception à Terre-Neuve, mais les engins de capture utilisés ne donnaient aucune information sur les juvéniles. Ici aussi, la bathymétrie apparaît donc comme un facteur déterminant dans la répartition de la population de crabe des neiges, puisque l'on observe aussi bien une augmentation de la taille qu'une diminution de la représentation de juvéniles avec la profondeur. Mais il apparaît que la nature granulométrique intervient également de façon importante pour perturber la monotonie de la répartition bathymétrique de l'espèce.

L'interprétation qui est faite de nos données peut toutefois être altérée par les biais induits par les méthodes d'échantillonnage. Les fonds très hétérogènes ne sont pas accessibles au chalut et le maillage utilisé sur les casiers ne retient pas les individus inférieurs à 45 mm, ce qui explique la faible quantité de femelles immatures recueillies avec cet engin. De plus, l'image de la population donnée par chacune des techniques de capture n'est pas identique. Le chalut utilisé serait efficace pour prélever les petits individus ; on a ainsi des crabes de moins de 30 mm de largeur de carapace en mai 1980 (fig. 5B). Mais il semble sous-représenter les plus gros qui, par leur mobilité, peuvent éviter l'engin. Dans les casiers, par contre, les grandes tailles sont beaucoup mieux représentées tandis que les plus petits individus peuvent s'échapper à travers les mailles. Ceci explique que, dans les résultats de l'analyse des correspon-

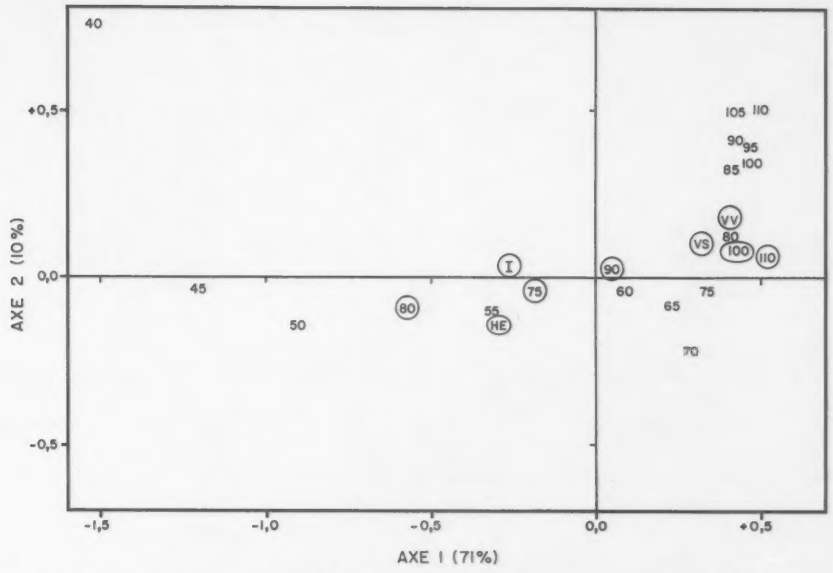


FIG. 8. Analyse des correspondances sur les distributions des mâles. Projection plane des classes de taille (chiffre simple) et des positions moyennes de paramètres écologiques : niveau bathymétrique et des classes de sédiment (chiffre encerclé) (HE = hétérogène envasé ; VS = vase sableuse ; VV = vase ; *I* = pourcentage d'immatures introduit en variable supplémentaire).

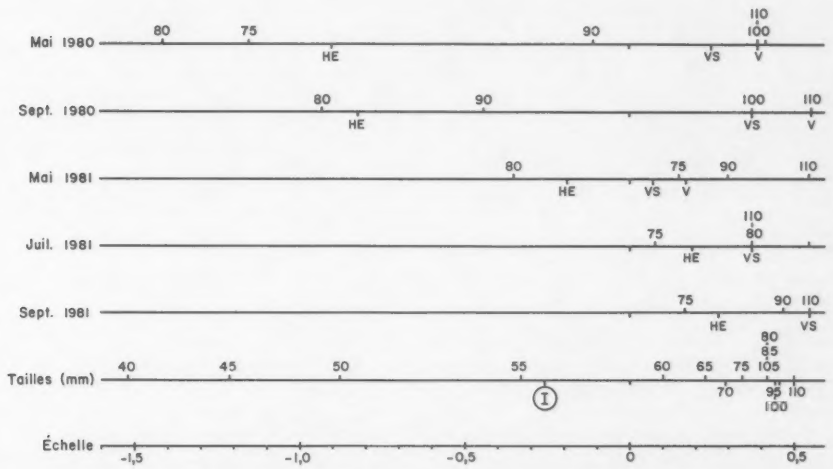


FIG. 9. Analyse des correspondances sur les distributions des mâles. Projection des classes de taille et des paramètres écologiques, pour chaque période d'échantillonnage, sur le premier axe factoriel (même légende que pour la fig. 8).

dances (fig. 9), les prélèvements effectués en mai 1980 sur les fonds de moins de 90 m soient plus fortement reliés aux petites tailles de mâles (moins de 55 mm) que les autres prélèvements. On peut expliquer ainsi la forte proportion de femelles immatures rencontrées à cette période. Mais on constate aussi que les données recueillies au casier en septembre 1980, bien que décalées vers les plus grandes tailles, donnent un schéma très semblable à celui de mai (fig. 5A, 5C et 9). Il est donc vraisemblable que les variations observées soient plus liées à des variations dans la population échantillonnée qu'à des biais liés aux engins.

Dans la ségrégation observée, il est difficile de séparer l'influence du gradient bathymétrique de celle de la granulométrie, les deux facteurs étant fortement corrélés. Mais on observe que l'augmentation de la profondeur ne joue pas un rôle important dans la répartition des juvéniles localisés sur les fonds hétérogènes, et ceux-ci abritent une plus forte proportion d'immatures que les autres substrats. Il apparaît donc que les jeunes individus prématures mâles, de 45 à 55 mm, se localisent préférentiellement sur ce type d'habitat. On peut supposer que les éléments grossiers du substrat puisse servir d'abri aux jeunes crabes contre leurs prédateurs. Après la métamorphose, les

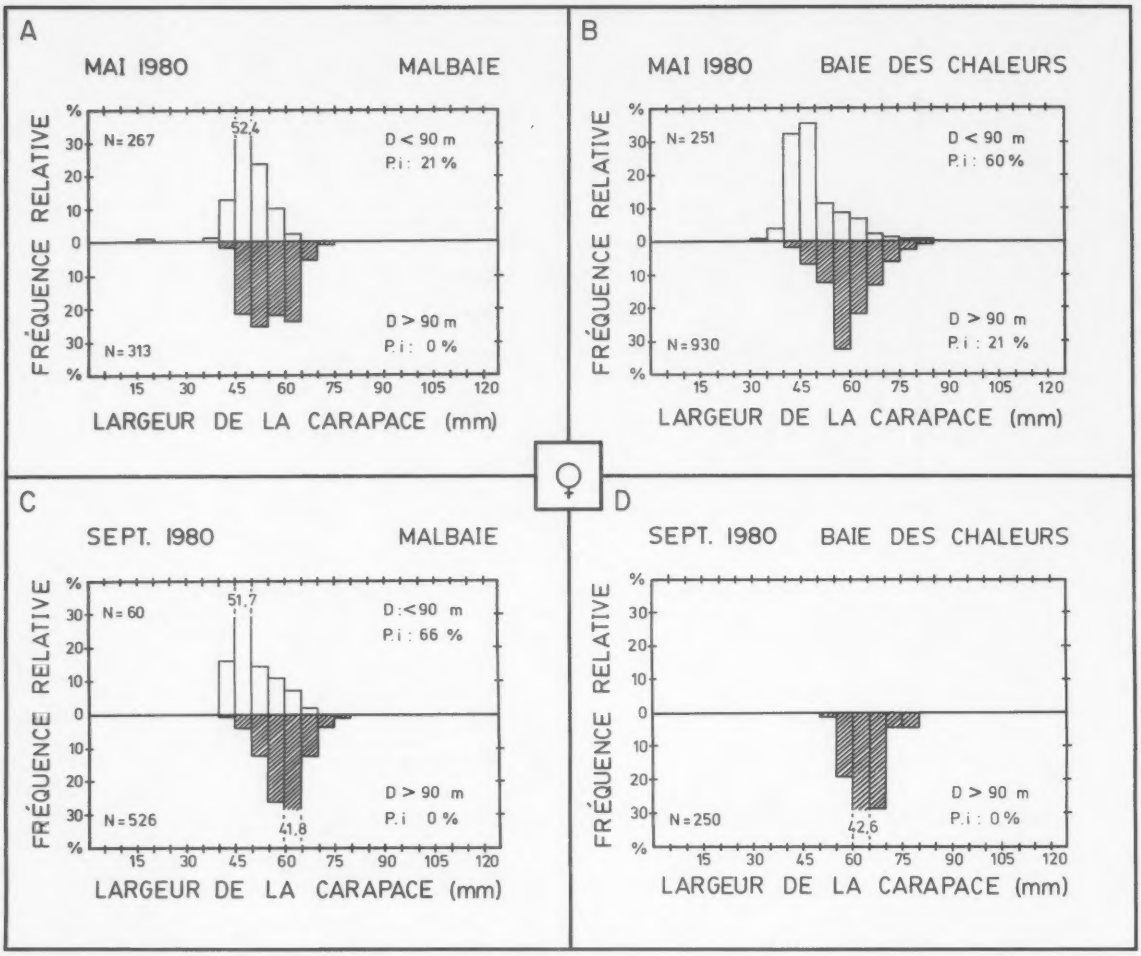


FIG. 10. Distribution des fréquences de la taille des femelles de *C. opilio* récoltées en 1980 (même légende que pour la fig. 5).

jeunes *C. opilio* sont soumis à une prédation intense (Bailey 1982 ; Waiwood et Elner 1982) et ceux qui sont localisés sur les substrats hétérogènes pourraient ainsi connaître un taux de survie plus élevé.

Le premier axe factoriel de l'analyse des correspondances paraît étirer les classes de taille des mâles selon leur degré de maturité sexuelle : à une extrémité l'on retrouve les individus totalement immatures, associés aux fonds hétérogènes, et à l'autre extrémité, les individus totalement matures (80 mm et plus) associés aux granulométries plus fines (fig. 8). Entre les deux se situe l'ensemble des individus pouvant être l'un ou l'autre et dont la situation paraît intermédiaire entre les différents substrats et niveaux bathymétriques. La taille de 60 mm, où 50 % des mâles sont physiologiquement matures, se situe en position moyenne, près de l'origine des axes, à proximité de la profondeur de 90 m, où les trois types de substrat peuvent être rencontrés et qui apparaît comme une véritable zone de transition. Au cours du cycle vital de *C. opilio* il y aurait ainsi un changement progressif d'habitat, des fonds hétérogènes vers les fonds plus vaseux, changement concomitant avec l'apparition de la maturité physiologique. Ceci paraît vérifié pour les mâles, mais seules les données récoltées en 1980 permettent d'avancer une semblable hypothèse pour les femelles.

L'étude du rapport des sexes indiquait une nette dominance des femelles en profondeur. Cette situation paraît reliée à l'activité de la pêche uniquement orientée vers les mâles de grande taille et principalement localisée sur ces types de fond. Une donnée reste la diminution de la part des femelles adultes entre mai et septembre sur les niveaux bathymétriques supérieurs (fig. 11) ce qui laisserait penser qu'elles quittent ces niveaux au cours de l'été.

## Mécanisme de recrutement

Le schéma général de la distribution de *C. opilio* tel qu'il est décrit suppose une descente des individus vers les zones plus profondes et plus vaseuses, au rythme des fréquences de mue. Pour les femelles, la mue de puberté s'effectue immédiatement avant l'accouplement qui a lieu à la fin de l'hiver puisque la copulation ne semble s'effectuer qu'entre une femelle à carapace molle et un mâle à carapace dure (Watson 1972). La descente vers les vasières doit donc se produire au cours de l'été,

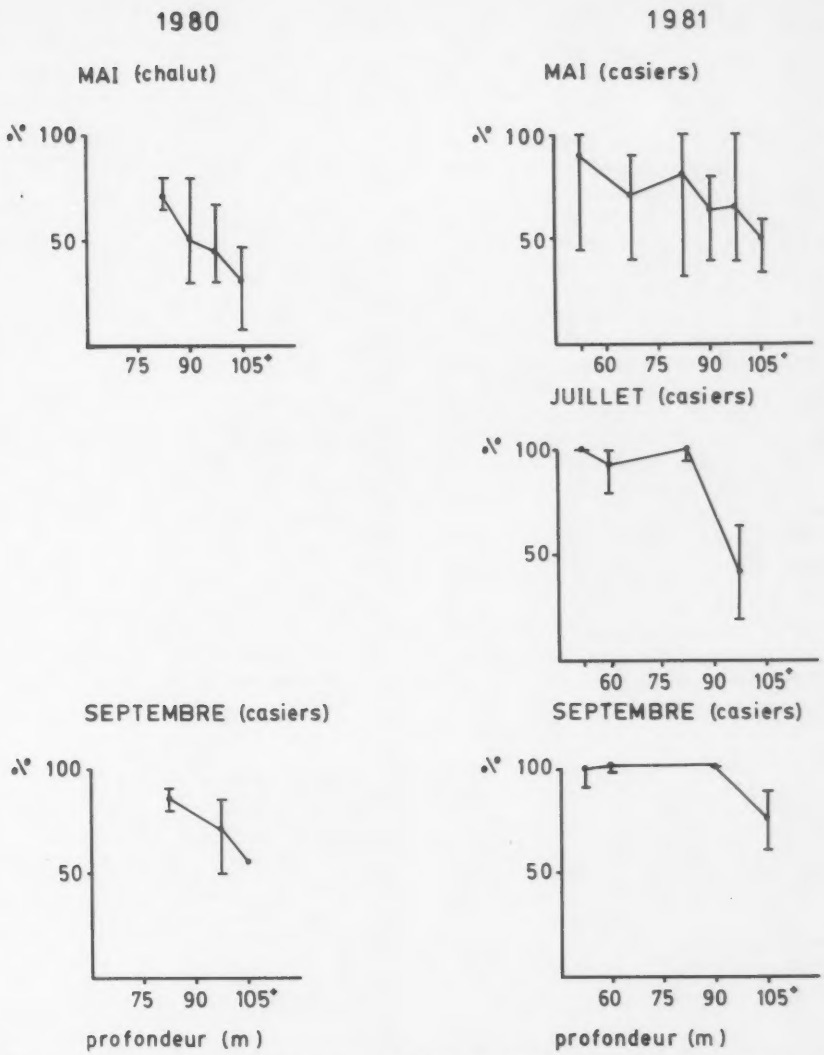


FIG. 11. Variation de la proportion des crabes mâles dans les échantillons, toutes régions confondues, l'intervalle indique les valeurs extrêmes rencontrées.

ce qui est vérifié par la diminution de l'abondance des femelles adultes entre mai et septembre sur les niveaux de faible profondeur. Le départ des femelles est observé aussi bien en 1980 qu'en 1981, année où il a été complété dès le mois de juillet. Par contre, la mue de maturation des mâles semble plutôt s'effectuer durant l'été (Watson 1969) et leur mouvement descendant devrait donc être décalé dans le temps par rapport à celui des femelles. La copulation à la fin de l'hiver sur des profondeurs relativement faibles suppose un mouvement de retour ascendant des mâles adultes. Ce type de migration génésique a été observé pour *C. tanneri* (Pereyra 1966) dont les mâles rejoignent les femelles en hiver pour la reproduction. Cette hypothèse pourrait être vérifiée par un échantillonnage plus serré dans le temps à la fin de l'hiver.

Kon (1969, 1980) a proposé un schéma de distribution de la population de *C. opilio* de la mer du Japon qui recoupe partiellement celui qui est proposé ici. Pour cet auteur, les stades précoces benthiques, très abondants aux profondeurs d'environ 375 m, effectuent une migration vers les fonds de 225 m où se concentrent les prématures. A ce niveau a lieu la mue de puberté et la copulation à laquelle fait suite une descente des femelles vers les fonds de 250–300 m et des mâles vers 325–375 m. Les profondeurs impliquées dans les deux systèmes, Japon et golfe du Saint-Laurent, sont extrêmement différentes, ce qui est sans doute à relier aux conditions hydrologiques des milieux concernés. Si nos données ne permettent pas d'hypothèse sur la localisation des plus jeunes stades benthiques, on note toutefois un élément commun important qui serait la localisation différente des prématures et de la zone d'accouplement, d'une part, et des adultes, d'autre part, selon un gradient bathymétrique. Les conditions locales de la partie du golfe du Saint-Laurent étudiée font qu'il se rajoute un élément granulométrique, élément qui apparaît ici très avantageux pour le crabe des neiges.

D'une façon générale, il apparaît que les individus prématures sont surtout localisés sur les fonds hétérogènes et associés à la communauté benthique à *Macoma calcarea*, et sur des fonds inférieurs à 90 m, tandis que les adultes sont surtout pêchés sur les fonds vaseux, plus profonds, de la communauté à *Maldane sarsi* et *Ophiura sarsi*. La différence dans les communautés benthiques associées au crabe se traduit d'ailleurs par une modification du régime alimentaire (Brêthes et al. 1985). Cette ségrégation observée entre les diverses composantes de la population de *C. opilio* peut revêtir une certaine importance pour la pêche. Les secteurs exploités sont situés au-dessous de la profondeur de 90 m c'est-à-dire, selon le schéma proposé, en dehors des zones d'abondance des prématures et d'accouplement. Il y aurait ainsi au moins une partie du recrutement à la pêche qui pourrait provenir des niveaux supérieurs non affectés par l'exploitation. Ce mécanisme de recrutement, ajouté à la sélection de la maille des casiers qui épargne les femelles et les plus petits mâles adultes, pourrait expliquer, partiellement du moins, la robustesse du stock de cette région qui a pu subir l'augmentation importante de l'effort de pêche de ces dix dernières années.

Certains points restent toutefois imprécis. Il n'est pas certain que ce schéma de distribution puisse être généralisé à l'ensemble du golfe bien que des augmentations de la taille du crabe avec les profondeurs soient mentionnées à Terre-Neuve (Miller et O'Keefe 1981), et sur la côte nord du golfe du Saint-Laurent (Greendale et Bailey 1982; F. Coulombe, P. E. Lafleur et J.-C. F. Brêthes, données non publiées). Enfin la répartition des stades précoces benthiques et les migrations génésiques des mâles adultes sont des aspects qu'il resterait à définir pour une meilleure compréhension de l'écologie de *C. opilio*.

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## Références

BAILEY, R. 1982. Relationship between catches of snow-crab, *C. opilio* (O. Fabricius), and abundance of cod (*Gadus morhua* L.) in the south western Gulf of St. Lawrence. Proc. Int. Symp. on the Genus *Chionoecetes*. Alaska Sea Grant Report 82-10: 485–497.

BELLAN, G. 1978. Contribution à l'étude des annélides polychètes de la province de Québec (Canada). 2. Étude synécologique. Théthys 8 (3) 1976: 231–240.

BENZECRI, J.-P., ET COLLABORATEURS. 1980. L'analyse des données. II. L'analyse des correspondances. 3e éd. Dunod, Paris. 632 p.

BRÊTHES, J.-C. F., G. DESROSIERS ET F. COULOMBE. 1985. Aspects de l'alimentation du comportement alimentaire du crabe des neiges (*Chionoecetes opilio* Fabr.) dans le sud-ouest du golfe du Saint-Laurent. Crustaceana. (Sous-presse)

BROWN, C. G., ET D. B. BENNETT. 1980. Population and catch structure of the edible crab (*C. pagurus*) in the English Channel. J. Cons. Cons. Int. Rxplor. Mer 39(1): 88–100.

BRUNEL, P. 1960. Observations sur la biologie et la biométrie du crabe-araignée *Chionoecetes opilio* Fabr. Rapport annuel 1960. Station de biologie marine de Grande-Rivière (Québec): 59–67.

1970. Aperçu sur les peuplements d'invertébrés marins des fonds meubles de la baie de Gaspé, 1956–60. Naturaliste C. 97: 679–710.

CHAPMAN, D. J. 1980. Ecology of juveniles and adults of *Nephrops*, p. 143–178. *Dans* The biology and management of lobsters. Vol. II. Academic Press, New York, NY.

COULOMBE, F. 1983. Ecologie et distribution d'une population de crabe-des-neiges, *Chionoecetes opilio*, dans le sud-ouest du Golfe du Saint-Laurent (Baie des Chaleurs). Mémoire de maîtrise, Université du Québec à Rimouski, Rimouski (Qué.). 123 p.

GREENDALE, R., ET R. J. F. BAILEY. 1982. Résultats d'inventaires du crabe-des-neiges (*Chionoecetes opilio*) dans l'estuaire et le golfe Saint-Laurent. Rapport tech. can. sci. halieut. aquat. 1099F: iii + 40 p.

HOWARD, A. E. 1980. Substrate control on the size composition of lobster (*Homarus gammarus*) population. J. Cons. Cons. Int. Explor. Mer 39(2): 130–133.

KANCIRUK, P. 1980. Ecology of juvenile and adult Palinuridae (Spiny lobster), p. 59–69. *Dans* The biology and management of lobsters. Vol. II. Academic Press, New York, NY.

KON, T. 1969. Fisheries biology of the Tanner crab. III. The density distribution and carapace width composition in relation to the depth. Bull. Jpn. Soc. Sci. Fish. 35(7): 624–628.

1980. Studies on the life history of the Zuwaii crab, *Chionoecetes opilio* (O. Fabr.). Special publication from the Sado Marine Biological Station, Nilgata University, Ser. 2: 1–64.

LAUZIER, L., ET W. B. BAILEY. 1957. Features of the deeper waters of the Gulf of St. Lawrence. Bull. Fish. Res. Board Can. 111: 213–250.

LAUZIER, L., R. N. TRITES ET H. B. HACHEY. 1957. Some features of the surface layer of the Gulf of St. Lawrence. Bull. Fish. Res. Board Can. 111: 195–212.

LEBART, L., ET J. P. FÉNELON. 1975. Statistique et informatique appliquées. Dunod, Paris. 439 p.

LEDOYER, M. 1975. Les peuplements benthiques circalittoraux de la baie des Chaleurs (Golfe du Saint-Laurent). Trav. Pêch. Qué. 42: 141 p.

LORING, D. H., ET D. J. G. NOTA. 1973. Morphology and sediments of the Gulf of St. Lawrence. Bull. Fish. Res. Board Can. 182: 147 p.

MILLER, R. J. 1975. Density of the commercial spider crab, *Chionoecetes opilio*, and calibration of effective area fished per trap using bottom photography. J. Fish. Res. Board Can. 32: 761–768.

MILLER, R. J., ET P. G. O'KEEFE. 1981. Seasonal and depth distribution, size, and molt cycle of the spider crabs, *Chionoecetes opilio*, *Hyas araneus*, and *Hyas coarctatus* in a Newfoundland bay. Can. Tech. Rep. Fish. Aquat. Sci. 1003: iv + 18 p.

PEREYRA, N. T. 1966. The bathymetric and seasonal distribution, and reproduction of adult tanner crab, *Chionoecetes tanneri* Rathbun, off the northern Oregon coast. Deep-Sea Res. 13(6): 1185–1205.

POWLES, H. W. 1968. Distribution and biology of the spider crab *Chionoecetes opilio* in the Magdalen Shallows, Gulf of St. Lawrence. Fish. Res. Board Can. Manuscr. Rep. 997: 106 p.

WAIWOOD, K. G., ET R. N. ELNER. 1982. Cod predation on snow crab (*Chionoecetes opilio*) in the Gulf of St. Lawrence. Proc. Int. Symp. on the Genus *Chionoecetes*. Alaska Sea Grant Report 82-10: 499–520.

WATSON, J. 1969. Biological investigation on the spider crab *Chionoecetes opilio*, p. 23–47. *Dans* Proc. Meeting on Atlantic Crab Fishery Development. Can. Fish. Rep. 13.

1970. Maturity, mating, and egg laying in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 27: 1607–1616.

1972. Mating behavior in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 29: 447–449.

# NOTES

# Effect of Dietary Calcium Phosphate and Zinc Supplementation on Whole Body Zinc Concentration of Rainbow Trout (*Salmo gairdneri*)[1]

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Hardy, R. W., and K. D. Shearer. 1985. Effect of dietary calcium phosphate and zinc supplementation on whole body zinc concentration of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 42: 181–184.

Groups of rainbow trout (*Salmo gairdneri*) were fed casein–gelatin diets supplemented with calcium phosphate ($Ca_3(PO_4)_2$) to produce dietary calcium and phosphorus levels of 1, 2, or 4% and 0.9, 1.5, or 2.4%, respectively (low, medium, or high calcium phosphate), and supplemented with 20 μg Zn/g diet as $ZnSO_4$, zinc proteinate, or $ZnSO_4$ + EDTA (1000 μg/g). Dietary calcium phosphate levels had no significant effect on weight gain of the fish, although the fish fed the high dietary calcium phosphate level were smaller than the rest. Dietary zinc supplementation had no effect on growth, but significantly increased whole body zinc levels in fish fed diets containing low or medium calcium phosphate. In fish fed diets containing low calcium phosphate, the zinc supplements all increased whole body zinc concentrations. In fish fed diets containing medium calcium phosphate, supplementation with zinc proteinate resulted in higher whole body zinc values than supplementation with other zinc sources. Dietary zinc supplementation did not increase whole body zinc concentrations above control levels in fish fed the experimental diets containing high calcium phosphate. We conclude that increased dietary levels of calcium phosphate reduced whole body zinc concentration of rainbow trout and that 20 μg Zn/g diet was insufficient to overcome this reduction at the highest dietary calcium phosphate level regardless of the form of zinc supplement used.

On a donné à des groupes de truites arc-en-ciel (*Salmo gairdneri*) des rations de caséine–gélatine additionnées de phosphate de calcium ($Ca_3(PO_4)_2$) de façon à obtenir des teneurs alimentaires en calcium et en phosphore respectives de 1, 2 ou 4 % et de 0,9, 1,5 ou 2,4 % (teneurs en phosphate de calcium faible, moyenne ou élevée) ; on a aussi ajouté aux aliments 20 μg Zn/g sous formes de $ZnSO_4$, de protéinate de zinc ou de $ZnSO_4$ + EDTA (1000 μg/g). Le phosphate de calcium n'a pas eu d'effet significatif sur le gain de poids des poissons, mais les poissons dont la nourriture en contenait une teneur élevée étaient plus petits. L'addition de zinc n'a pas eu d'effet sur la croissance, mais l'on a noté des teneurs en zinc significativement plus élevées dans tout l'organisme des poissons dont la nourriture avait une teneur en phosphate faible ou moyenne. Toutes les additions de zinc se sont traduites par des concentrations de zinc plus élevées dans tout l'organisme des poissons dont la nourriture contenait une faible teneur en phosphate de calcium. Chez les poissons dont la nourriture contenait une concentration moyenne de phosphate de calcium, l'addition de protéinate de zinc s'est traduite par des teneurs en zinc dans l'organisme entier plus élevées que celles résultant de l'addition de zinc sous les autres formes. L'addition de zinc ne s'est pas traduite, chez les poissons dont la nourriture contenait la concentration élevée de phosphate de calcium, par des concentrations de zinc dans l'organisme entier supérieure aux concentrations notées chez les témoins. Nous en concluons que les teneurs alimentaires en phosphate de calcium plus élevées ont provoqué une réduction de la concentration de zinc dans l'organisme entier chez la truite arc-en-ciel et qu'une teneur alimentaire de zinc de 20 μg/g ne suffisait pas à faire disparaître cette réduction à la teneur alimentaire de phosphate de calcium la plus élevée, ceci quelle que soit la forme du zinc ajouté.

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The dietary zinc requirement of rainbow trout (*Salmo gairdneri*) fed purified diets has been reported to be 15–30 μg/g (Ogino and Yang 1978). Zinc deficiency in rainbow trout has resulted in poor growth, high mortality, lens cataracts, and reduced whole body and tissue zinc levels (Ogino and Yang 1978; Satoh et al. 1983). Dietary zinc availability can apparently be reduced by other dietary ingredients or nutrients in fish diets. Ketola (1979) found that in a practical diet containing high-ash white fish meal, 60 μg dietary Zn/g diet was not enough to prevent poor growth and cataracts in rainbow trout. He also found that adding extra calcium, phosphorus, sodium, and potassium to this diet increased the incidence and severity of cataracts. Dietary supplementation of 150 μg Zn/g diet in the white-fish meal diet overcame these problems. Spinelli et al. (1983) reported that the availability of dietary zinc in purified rainbow trout diets was reduced when dietary levels of calcium and magnesium were increased.

There is a trend toward increased utilization in human food products, such as surimi, of some fish previously used to make fish meal. A result of this trend is an increased use of white fish meal in place of fish meals made from whole fish, such as herring (*Clupea harengus*), in salmonid diets. The concentrations of calcium and phosphorus are elevated in high-ash white fish meals (National Research Council 1981). The use of high-ash white fish meals in salmonid diets is a concern, especially since high dietary ash levels have been linked with the high incidence of cataracts in salmon smolts, *Oncorhynchus kisutch* and *O. tshawytscha*, in Pacific Northwest salmon hatcheries in 1981 (D. Roley, Washington Department of Fisheries, Seattle, WA, pers. comm.). Our experiment was designed to examine the effects of dietary supplementation with calcium phosphate ($Ca_3(PO_4)_2$) and three zinc sources on whole body zinc levels of rainbow trout fed semipurified diets.

TABLE 1. Basic composition of experimental diets used to test the effects of supplemental $Ca_3(PO_4)_2$ and zinc on whole body zinc concentrations of rainbow trout.

| Ingredient | g/kg diet |
|---|---|
| Vitamin-free casein | 260.0 |
| Gelatin | 52.5 |
| Pregelatinized wheat starch | 23.5 |
| Carboxyl methyl cellulose | 5.0 |
| Dextrin[a] | 74.0, 62.0, 38.0 |
| Vitamin premix[b] | 10.0 |
| 70% choline chloride | 5.0 |
| Soybean oil | 52.0 |
| L-Methionine | 4.0 |
| L-Tryptophan | 2.0 |
| $Ca_3(PO_4)_2$[c] | 12.0, 24.0, 48.0 |
| Trace mineral solution[d] | 100 mL |
| Zinc supplement[e] | — |
| Water | 400 mL |

[a]Dextrin replaced as required by $Ca_3(PO_4)_2$.

[b]Vitamin premix supplied the following per kilogram of diet: 141 mg calcium D-pantothenate; 41 mg pyridoxine-HCl; 111 mg riboflavin; 293 mg niacinamide; 17 mg folic acid; 57 mg thiamin mononitrate; 0.79 mg biotin; 0.08 mg vitamin $B_{12}$; 15 mg menadione sodium bisulfite; 668 mg α-tocopheryl acetate; 8800 IU vitamin A palmatate or acetate; 352 mg myoinositol; 1188 mg ascorbic acid; 660 IU vitamin $D_3$.

[c]$Ca_3(PO_4)_2$: 2.4% added to diets 1–4, 4.8% to diets 5–8, and 9.6% to diets 9–12 on a dry weight basis.

[d]Trace mineral solution supplied the following per kilogram of diet: 27 mg Mn; 265 mg Fe; 9.7 mg Cu; 0.9 mg Co; 2934 mg Mg; 10 mg I; 5995 mg Na.

[e]20 μg Zn/g diet added as $ZnSO_4$ in diets 2, 6, 10; zinc proteinate in diets 3, 7, 11; $ZnSO_4$ + 1000 μg EDTA/g diet in diets 4, 8, 12.

## *Materials and Methods*

Groups of 125 rainbow trout (mean weight 1.1 g) were randomly distributed into 12 circular, polypropylene, indoor, 200-L tanks. Each tank was aerated and supplied with 2.4 L/min of constant-temperature (15°C) dechlorinated city water. A natural photoperiod was used. Fish in each tank were bulk weighed and counted every 21 d for 84 d. At the end of the experiment, the fish in each tank were individually weighed.

Twelve experimental diets based on the Oregon Test Diet (National Research Council 1973) were formulated and fed in a 3 × 4 factorial design. The basal diet (Table 1) was modified by adding calcium phosphate at the expense of dextrin to produce diets containing 1% calcium and 0.9% phosphorus (low calcium phosphate), 2% calcium and 1.5% phosphorus (medium calcium phosphate), and 4% calcium and 2.4% phosphorus (high calcium phosphate). Nine of the diets were then fortified with 20 μg Zn/g diet as either $ZnSO_4$, zinc proteinate,[2] or $ZnSO_4$ + 1000 μg ethylenediaminetetraacetic acid (EDTA)/g diet. The basal diet contained 35 μg Zn/g diet. Each diet was mixed, pelleted by extrusion, and stored frozen at −20°C until fed.

The amount of feed supplied to the fish was determined by the method of Buterbaugh and Willoughby (1967) using a hatchery constant of 16. The trout were hand-fed four times per day, and the feeding rate was adjusted weekly based on projected growth. Each week the fish received 7 d of rations in 5 d.

Proximate and elemental composition of samples of each diet and of individual fish from each dietary treatment were determined. Diet samples were collected at the beginning of the experiment. At the termination of the experiment (day 84), 10 fish weighing within 1 standard deviation of the mean were selected from each treatment for elemental analysis. Proximate composition was determined using conventional procedures (Association of Official Analytical Chemists 1975). Elemental composition was determined using procedures described previously by Hardy et al. (1983). Digestible energy values were calculated using values of 16.7, 33.5, and 8.4 kJ/g for protein, fat, and carbohydrate, respectively (Jobling 1983).

Analysis of variance was performed on final weight and whole body zinc concentration data. Scheffe's test and Duncan's new multiple range test were used to test for significance ($P < 0.05$) between treatment means for final weight and whole body zinc concentration, respectively (Zar 1974).

## *Results*

Dietary supplementation with calcium phosphate increased the dry weight ash levels from 5.4% in the low calcium phosphate diet to 7.8 and 12.6% for the medium and high calcium phosphate diets, respectively. Replacement of dextrin with calcium phosphate slightly decreased the calculated digestible energy contents of the diets from 14 677 kJ/kg in the

[2]Zinc amino acid chelate, Albion Laboratories, Clearfield, UT 84015, USA.

TABLE 2. Apparent zinc retention values (%) calculated at the end of the experiment.[a]

| Dietary Zn source | Dietary $Ca_3(PO_4)_2$ level (%) 2.4 | 4.8 | 9.6 |
|---|---|---|---|
| No supplemental Zn | 36 | 32 | 22 |
| $ZnSO_4$ (20 μg Zn/g diet) | 35 | 29 | 19 |
| Zinc proteinate (20 μg Zn/g diet) | 47 | 30 | 18 |
| $ZnSO_4$ + EDTA (20 μg Zn/g diet) | 36 | 29 | 19 |

[a]Apparent zinc retention (%) = (mg Zn in fish at end of experiment − mg Zn in fish at beginning of experiment)/(mg Zn fed per fish during experiment).

low calcium phosphate diet to 14 477 and 14 075 kJ/kg for the medium and high calcium phosphate diets, respectively. Weight gains were not significantly affected ($P > 0.05$) by dietary calcium phosphate. The average weights of the fish fed diets containing low, medium, or high calcium phosphate were 8.75, 7.65, and 7.30 g, respectively. Dietary zinc supplementation also did not significantly affect final fish weight ($P > 0.05$). The mean values were 7.47 g for fish fed diets not supplemented with zinc, 8.00 g for fish fed diets supplemented with $ZnSO_4$, 7.67 g for fish fed diets supplemented with zinc proteinate, and 8.50 g for fish fed diets supplemented with $ZnSO_4$–EDTA. Food conversion values averaged 0.89 (dry food fed/wet fish weight gain) and were not significantly affected by dietary treatment. Apparent zinc retention was reduced in a stepwise manner at each level of dietary calcium phosphate supplementation (Table 2). At each level of dietary calcium phosphate supplementation, similar apparent zinc retention values between dietary zinc treatments were observed with the exception of zinc proteinate in the low calcium phosphate diet. Proximate composition of the rainbow trout was similar between dietary treatments (data not shown).

Whole body zinc concentrations were significantly affected by dietary treatment (Table 3). Fish fed diets containing low calcium phosphate without zinc supplementation had significantly lower whole body zinc levels ($P < 0.05$) than fish fed zinc-supplemented diets. The source of supplemental zinc did not affect whole body zinc levels among fish fed diets containing low calcium phosphate. Increasing the dietary calcium phosphate level reduced whole body zinc levels of all dietary groups compared with the low calcium phosphate treatments except in the group fed the diet supplemented with zinc proteinate. Some differences were noted between groups receiving zinc supplementation in the medium calcium phosphate diets. The zinc content of fish fed diets containing high calcium phosphate was not significantly affected by dietary zinc supplementation, regardless of the source. In trout fed diets supplemented with zinc, whole body body zinc levels were significantly reduced ($P < 0.05$) in groups fed the high calcium phosphate diets compared with the treatment groups of fish fed diets containing low or medium calcium phosphate.

No cataracts were observed in fish from any of the experimental treatment groups.

## *Discussion*

Our results showed that whole body levels of zinc were significantly reduced in rainbow trout fed a semipurified diet containing high levels of calcium and phosphate. This reduction was presumably due to reduced zinc availability in the high calcium phosphate diets. Efforts to increase zinc availability by chelation were only partially successful. Adding 1000 μg EDTA (0.1%)/g diet to the diets supplemented with $ZnSO_4$ did not result in any differences in whole body zinc concentrations at any dietary calcium phosphate level compared with adding $ZnSO_4$ alone. Weight gains were slightly increased in the $ZnSO_4$–EDTA supplemented diets, perhaps due to a beneficial effect of EDTA on the availability of some trace element other than zinc. Other studies in our laboratory were also unable to measure any effect on whole body zinc levels of EDTA supplementation (100 μg/g) to rainbow trout diets containing soybean meal (J. C. Wekell and K. D. Shearer, unpubl. data). Dietary supplementation with zinc proteinate seemed effective at maintaining whole body zinc levels when the dietary calcium phosphate level was increased from low to medium. However, an additional increase in dietary calcium phosphate to the high level significantly reduced whole body zinc levels in all treatments, including zinc proteinate. Supplementing diets with a biologically available, chelated element should insure an adequate level of absorption in the presence of dietary compounds that interfere with absorption of the cation. If the zinc proteinate had been more available than the other dietary zinc supplements, the whole body zinc levels of rainbow trout fed diets containing high calcium phosphate should have been higher in fish fed diet 11 compared with diet 10 or 12.

Despite the significantly lower whole body zinc concentrations in trout fed diets containing the high level of calcium phosphate, no deficiency signs were observed. Ogino and Yang (1978) found that trout exhibiting zinc deficiency signs had whole body zinc levels of 28–32 μg/g dry weight compared with whole body zinc levels of 72–77 μg/g in fish fed diets containing adequate amounts of zinc. In our study, whole body levels were reduced to 41–48 μg/g in trout fed the high calcium phosphate diets. It is likely that the length of our study was insufficient to reduce whole body zinc levels in fish fed the high

TABLE 3. Whole body zinc concentration (μg/g dry wt ± SE) of the rainbow trout at the end of the experiment. Values followed by the same letter are not significantly different ($P > 0.05$).

| Dietary Zn source | Dietary $Ca_3(PO_4)_2$ level (%) 2.4 | 4.8 | 9.6 |
|---|---|---|---|
| No supplemental Zn | 57.4±3.5 bcd | 46.0±3.5 ed | 41.4±4.6 f |
| $ZnSO_4$ (20 μg Zn/g diet) | 80.9±3.7 a | 55.3±2.4 cde | 44.5±3.0 f |
| Zinc proteinate (20 μg Zn/g diet) | 87.6±2.0 a | 79.5±3.2 a | 45.3±1.4 ef |
| $ZnSO_4$ + EDTA (20 μg Zn/g diet) | 77.8±3.0 a | 59.3±3.6 bc | 47.9±1.5 def |

calcium phosphate diets to levels at which overt deficiency signs would appear.

Numerous studies with a variety of terrestrial animals have shown that the biological availability of dietary zinc can be reduced by supplemental calcium (Lewis et al. 1956; Hoekstra 1964; Robertson and Schaible 1960), calcium and phytic acid (O'Dell et al. 1964; Likuski and Forbes 1964), and calcium phosphate in the absence of phytic acid (Cabell and Earle 1965; Heth et al. 1966). Calcium phosphates have been shown in vitro to precipitate from solutions when the pH is increased from 3 to 6, removing zinc from solution in the process (Lewis et al. 1957). Zinc availability is thought to be reduced in vivo by absorption of zinc on insoluble calcium phosphate complexes in the intestine, which are then passed through the gut and excreted. This and other zinc-complexing processes can often be avoided by adding chelating agents to the diet (O'Dell 1972; Vohra and Kratzer 1964; Kratzer et al. 1959; Suso and Edwards 1968).

Ketola (1979) showed that the bioavailability of zinc in rainbow trout diets is reduced by high-ash white fish meal. He also demonstrated that the severity and incidence of deficiency signs was increased when additional calcium, phosphorus, sodium, and potassium were added to the white fish meal based trout diets. Our results indicate that calcium and phosphorus, the main constituents of high-ash fish meal, can be major factors in reducing zinc availability in rainbow trout diets.

The dietary calcium and phosporus levels used in this experiment approximately cover the range of values reported to occur in commercial fish feeds. Tacon and DeSilva (1983) found that the ranges of calcium and phosphorus in trout feed in Europe were 1.3–3.7% and 0.9–2.8%, respectively. Commercial salmonid feeds in North America typically have calcium and phosphorus levels that range from 2.2 to 4.2% and 1.2 to 2.6%, respectively (R. W. Hardy and K. D. Shearer, unpubl. data). Thus, the reduction in whole body zinc concentration we observed may occur in practical salmonid diets that contain high-ash fish meal. Many commercial fish feeds use ingredients that contain phytic acid, and forms of fiber that may further reduce zinc bioavailability. Therefore, the potential for reduction of zinc availability in practical salmonid diets may be greater than that we have seen in this experiment. The approach of some agencies responsible for establishing ingredient specifications for trout and salmon diets has been to restrict the use of high-ash fish meal. Practical considerations may force agencies to allow the use of high-ash fish meals in formulations as long as trace element fortification is increased. Before this approach is implemented, a more thorough understanding is needed of the factors that can reduce trace element availability in fish feeds.

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*References*

Association of Official Analytical Chemists. 1975. Official methods of analysis. 12th ed. Assoc. Off. Anal. Chem., Washington, DC. 1094 p.

Butterbaugh, G. L., and H. Willoughby. 1967. A feeding guide for brook, brown, and rainbow trout. Prog. Fish-Cult. 77: 210–215.

Cabell, C. A., and I. P. Earle. 1965. Additive effects of calcium and phosphorus in utilization of dietary zinc. J. Anim. Sci. 24: 800–804.

Hardy, R. W., K. D. Shearer, F. E. Stone, and D. H. Wieg. 1983. Fish silage in aquaculture diets. J. World Maricult. Soc. 14: 695–703.

Heth, D. A., W. M. Becker, and W. G. Hoekstra. 1966. Effect of calcium, phosphorus, and zinc or zinc-65 absorption and turnover in rats fed semipurified diets. J. Nutr. 88: 331–337.

Hoekstra, W. G. 1964. Recent observations on mineral interrelationships. Fed. Proc. 23: 1068–1076.

Jobling, M. 1983. A short review and critique of methodology used in fish growth and nutrition studies. J. Fish Biol. 23: 685–703.

Ketola, H. G. 1979. Influence of dietary zinc on cataracts in rainbow trout (*Salmo gairdneri*). J. Nutr. 109: 965–969.

Kratzer, F. H., J. B. Allred, P. N. Davis, B. J. Marshall, and P. Vohra. 1959. The effect of autoclaving soybean protein and the addition of ethylenediaminetetraacetic acid on the biological availability of dietary zinc for turkey poults. J. Nutr. 68: 313–322.

Lewis, P. K. Jr., R. H. Grummer, and W. G. Hoekstra. 1957. The effect of method of feeding upon the susceptibility of the pig to parakeratosis. J. Anim. Sci. 16: 927–936.

Lewis, P. K. Jr., W. G. Hoekstra, R. H. Grummer, and P. H. Phillips. 1956. The effect of certain nutritional factors including calcium, phosphorus, and zinc in parakeratosis in swine. J. Anim. Sci. 15: 741–751.

Likuski, H. J. A., and R. M. Forbes. 1964. Mineral utilization of the rat. IV. Effects of calcium and phytic acid on the utilization of dietary zinc. J. Nutr. 84: 145–148.

National Research Council. 1973. Nutrient requirements of trout, salmon, and catfish. National Academy of Sciences, Washington, DC. 57 p.

1981. Nutrient requirements of coldwater fishes. National Academy of Sciences, Washington, DC. 63 p.

O'Dell, B. L. 1972. Dietary factors that affect biological availability of trace elements. Ann. N.Y. Acad. Sci. 199: 70–81.

O'Dell, B. L., J. M. Yohe, and J. E. Savage. 1964. Zinc availability in the chick as affected by phytate, calcium, and ethylenediaminetetraacetate. Poult. Sci. 43: 415–419.

Ogino, C., and C-Y. Yang. 1978. Requirements of rainbow trout for dietary zinc. Bull. Jpn. Soc. Sci. Fish. 44: 1015–1018.

Robertson, R. H., and P. J. Schaible. 1960. The effect of elevated calcium and phosphorus levels on the zinc requirement of the chick. Poult. Sci. 39: 837–840.

Satoh, S., T. Takiuchi, Y. Narabe, and T. Watanabe. 1983. Effects of deletion of several trace elements from fish meal diets on growth and mineral composition of rainbow trout fingerlings. Bull. Jpn. Soc. Sci. Fish. 49: 1909–1916.

Spinelli, J., C. R. Houle, and J. C. Wekell. 1983. The effect of phytates on the growth of rainbow trout (*Salmo gairdneri*) fed purified diets containing varying quantities of calcium and magnesium. Aquaculture 30: 71–83.

Suso, F. A., and H. M. Edwards, Jr. 1968. Influence of various chelating agents on absorption of $^{60}Co$, $^{59}Fe$, $^{54}Mn$, and $^{65}Zn$ by chickens. Poult. Sci. 47: 1417–1425.

Tacon, A. G. J., and S. S. DeSilva. 1983. Mineral composition of some commercial fish feeds available in Europe. Aquaculture 31: 11–20.

Vohra, P., and F. H. Kratzer. 1964. Influence of various chelating agents on the availability of zinc. J. Nutr. 82: 249–256.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, NJ. 620 p.

# Effects of Dietary 17α-Methyltestosterone and Bovine Growth Hormone on Growth and Food Conversion of Slow- and Normally-Growing American Elvers (*Anguilla rostrata*)

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Degani, G., and M. L. Gallagher. 1985. Effects of dietary 17α-methyltestosterone and bovine growth hormone on growth and food conversion of slow- and normally-growing American elvers (*Anguilla rostrata*). Can. J. Fish. Aquat. Sci. 42: 185–189.

Dietary addition of 17α-methyltestosterone (MT) and bovine growth hormone (bGH) had a significant effect on growth and food conversion in American elvers (*Anguilla rostrata*). Both MT (1 μg/g) and bGH (2 and 10 μg/g) significantly increased the mean weight of elvers compared with controls. Higher concentrations of MT (10 μg/g) increased mean body weight, but not significantly. The effects of MT were more pronounced in normally-growing elvers compared with slow-growing elvers. Reduction of water temperature had a much stronger influence on weight gain in slow-growing elvers receiving MT than with normally-growing eels receiving MT. Food conversion was improved by feeding either MT or bGH. Food conversion was generally lower in slow-growing than in normally-growing elvers. Total body protein was related to body weight and was significantly lower in elvers fed MT than in control elvers. However, there was no significant difference in total body protein elvers fed bGH compared with the control group.

L'addition de 17α-méthyltestostérone (MT) et d'hormone de croissance bovine (HCb) a la nourriture de jeunes anguilles d'Amérique (*Anguilla rostrata*) a eu un effet appréciable sur leur croissance et leur conversion alimentaire. Le MT (1 μg/g) et la HCb (2 et 10 μg/g) ont tous deux produit une augmentation significative du poids moyen des jeunes anguilles, comparativement à celui des témoins. La concentration la plus élevée de MT (10 μg/g) s'est traduite par une augmentation du poids moyen qui n'était cependant pas significative. Les effets du MT étaient plus prononcés chez les jeunes anguilles à croissance normale que chez celles à croissance lente. Chez les sujets à nourriture enrichie de MT, l'abaissement de la température de l'eau a influé beaucoup plus fortement sur le gain de poids de ceux à croissance lente, comparativement à ceux à croissance normale. La présence dans la nourriture de MT ou de HCb améliorait la conversion alimentaire, et celle-ci était généralement plus faible chez les anguilles à croissance lente que chez celles à croissance normale. La teneur totale en protéines présentait une relation avec le poids et était significativement plus faible chez les jeunes anguilles recevant du MT que chez les témoins. Cette différence n'a cependant pas été notée pour les jeunes anguilles dont la nourriture contenait de la HCb.

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Factors critical to growth of American eels (*Anguilla rostrata*) during the initial period of elver culture are mostly unknown. The initial period of elver culture is characterized by a high mortality rate and major differences in growth rate of individual eels (Degani and Levanon 1983). Because slow-growing elvers have little economic value (Liewes 1978; Degani and Levanon 1983), an understanding of the factors that control growth rate is essential for the further development of commercial eel operations.

Growth of fish can be stimulated by hormones. Thyroid hormones and androgens (Higgs et al. 1982) as well as growth hormones (Donaldson et al. 1979) induce increased growth. However, most often these hormones are administered by injection rather than through the diet. In addition, very little attention has been directed to the study of the effects of growth-stimulating hormones on slow-growing fish. Hence, the purpose of our study was to investigate the effects of dietary bovine growth hormone and 17α-methyltestosterone on growth, food conversion, and body composition of elvers with varying growth rates.

## *Materials and Methods*

American elvers were netted during spring migration and held for approximately 7 mo at East Carolina University's (ECU) Estuarine Laboratory in Aurora, NC. They were then transported to the nutrition laboratory on the ECU campus in Greenville, NC, acclimated in aquaria for 1 wk, and checked for

disease. The elvers were then divided into four size groups by weight: fast-growing (F) (1.75 ± 0.25 g), moderate-growing (M) (0.72 ± 0.25 g), slow-growing (S) (0.25 ± 0.15 g), and slowest-growing (V) (0.15 ± 0.05 g). Each group was separated randomly into control and experimental groups with three replicates in each group. There was no significant difference between the weights of control and experimental groups at the beginning of the experiment ($t$-test, $p < 0.05$).

The basal diet we used was a premixed feed for eels obtained from Ruva Holland, 6710 Be EDE-Holland. The analysis of the dry diet was 12% ash, 51% protein, and 17% crude fat. Androgen (17α-methyltestosterone (MT), Aldrich Company, Inc.) was dissolved in cod liver oil and then mixed with the basal diet and water to form a dough. Final concentration of MT in moist dough was 1 or 10 μg/g wet wt. Bovine growth hormone (bGH) (Upjohn Company) was dissolved in 0.7% NaCl with pH adjusted to 9.5 using 0.07 mol NaOH/L (Higgs et al. 1975). The hormone was mixed with the basal diet and water to form doughs with final concentrations of 2 and 10 μg/g wet wt. Control diets were prepared in the same manner as the hormone diets. Moisture content of all dough diets was 50% of total wet weight. All food was stored at −10°C.

M and V elvers were used to test the effect of bGH at 10 and 2 μg/g, respectively. MT was tested in F, M, and S groups at 1 and/or 10 μg/g. There were three replicates at each hormone level and three replicates of nontreated controls for each size group. The hormone treatment, size group, and number of fish in each replicate of each test group were as follows: MT (10 μg/g), group F, 3 fish; MT (1 μg/g), group F, 7 fish; MT (1 μg/g), group M, 6 fish; MT (1 μg/g), group S, 10 fish; bGH (10 μg/g), group M, 3 fish; bGH (2 μg/g), group S, 20 fish.

All elvers were fed at 7% of total live body weight daily (dry weight of food to wet weight of fish). One half of the food was fed at 07:00 and the other half at 19:00. Maximum and minimum temperatures were recorded daily. Ammonia and chloride levels were monitored daily and remained below 1 and 2 mg/L, respectively. Nitrate levels were monitored weekly and never exceeded 2 mg/L. Gross feed conversion efficiency (grams food fed per gram weight gain) was calculated for each replicate group (Windell 1978) for the first 10 d of the feeding trial. We used a $t$-test to test for significant differences between mean weights of experimental groups and controls.

## *Results*

In all size groups, elvers fed 1 μg MT/g grew significantly faster ($p < 0.05$) than controls after 12 and 21 d (Fig. 1). The influence of MT treatment on growth of M and F elvers appeared to be greater than the influence of MT on growth of S elvers.

During the experiment, temperature in the culture tanks decreased steadily from day 3 to day 15 (Fig. 1) and slowed growth in all elvers. However, the effect appeared to be more pronounced in the S elvers.

MT (1 μg/g) treatment improved food conversion in all experimental groups compared with controls (Table 1). Total body protein was significantly lower ($p < 0.05$) in elvers receiving MT in their diets compared with the control (Table 2). Total body protein was related to body weight, as is usually found in growing animals (Klieber 1975; Gallagher et al. 1984). When F elvers were fed diets with 10 μg MT/g, mean body weight appeared to increase, but this increase was not significant (Fig. 2).

bGH (2 μg/g) caused a significant increase ($p < 0.05$) in

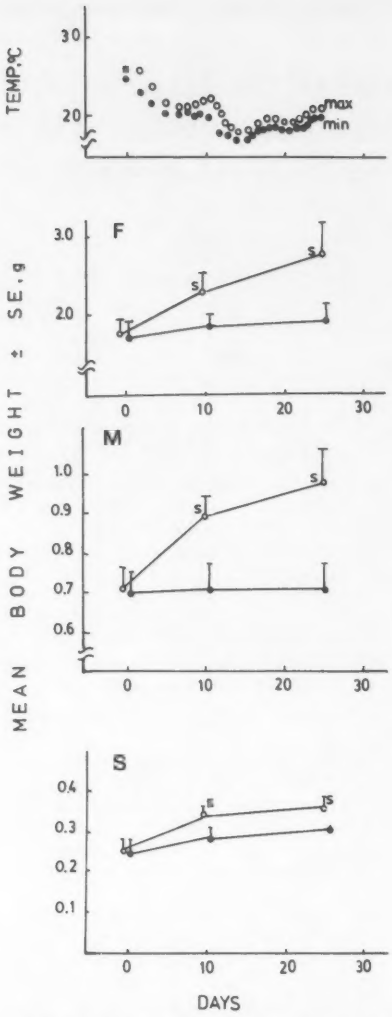


FIG. 1. Changes in mean body weight in S, M, and F elvers treated with 1 μg MT/g (○) or untreated controls (●). Superscript $s$ indicates a significant difference ($t$-test, $p < 0.05$) between weights of control and treated elvers at a specific time period.

TABLE 1. Gross food conversion efficiency (first 10 d) for the experimental groups of elvers with hormone treatment. Ration level was 7% of body weight on a dry food to wet weight basis.

| Experimental group | Gross food conversion efficiency (g food fed/g weight gain) |
|---|---|
| V (2 μg bGH/g) | 1.43 |
| V (control) | 2.53 |
| S (1 μg MT/g) | 1.23 |
| S (control) | 1.76 |
| M (1 μg MT/g) | 1.90 |
| M (control) | 3.79 |
| F (1 μg MT/g) | 2.03 |
| F (control) | 3.21 |

TABLE 2. Effect of dietary MT and bGH on total body protein in different size eels.

| Experimental group | N | % protein (mean ± SD) | p |
|---|---|---|---|
| M (1 μg MT/g) | 10 | 46.92±6.53 | <0.05 |
| M (control) | 10 | 52.18±2.56 | |
| S (1 μg MT/g) | 6 | 50.25±1.71 | <0.05 |
| S (control) | 6 | 52.50±1.29 | |
| V (2 μg bGH/g) | 6 | 53.33±4.13 | >0.05 |
| V (control) | 6 | 54.00±2.00 | |

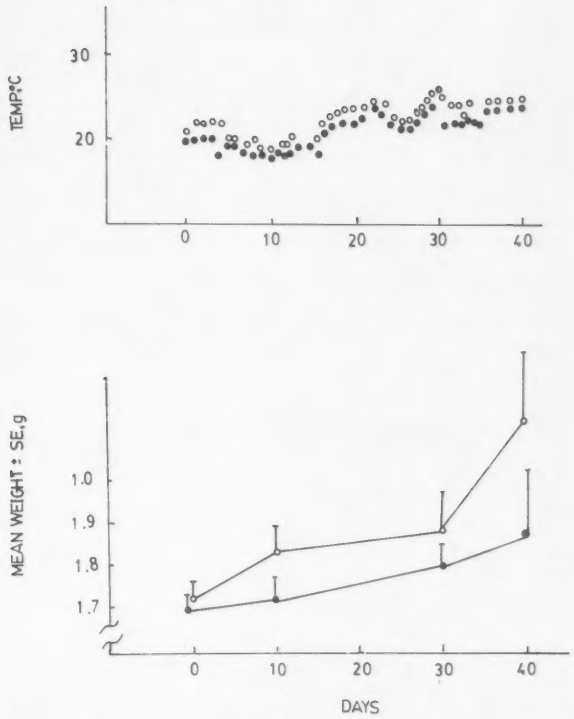


FIG. 2. Changes in mean body weight of F elvers treated with 10 μg MT/g (○) or untreated controls (●).

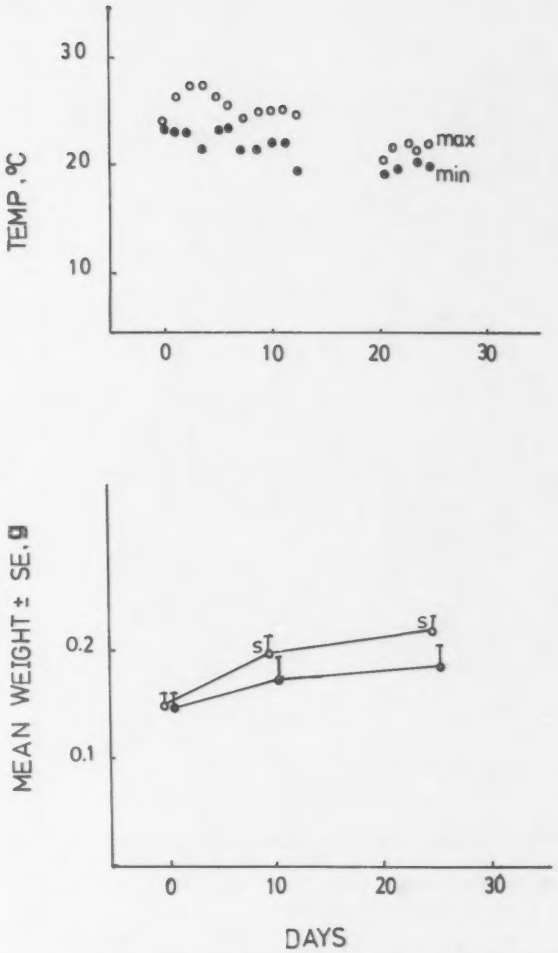


FIG. 3. Changes in mean body weight of V elvers fed 2 μg bGH/g (○) or untreated controls (●). Superscript *s* indicates a significant difference (*t*-test, $p < 0.05$) between weights of control and treated elvers at a specific time period.

weight of V elvers at 10 and 21 d compared with control groups (Fig. 3). The decrease in temperature affected both control and treated elvers (Fig. 3) but was less in control groups of larger elvers (Fig. 1). Compared with control groups, gross food conversion efficiency was improved in elvers fed dietary bGH at 2 μg/g (Table 1). There was no significant difference in total body protein between hormone-treated and control elvers. When M elvers were fed diets containing 10 μg bGH/g, mean body weight was significantly increased ($p < 0.05$) after 30 d (Fig. 4).

*Discussion*

Androgens are known to influence growth of coho salmon, *Oncorhynchus kisutch* (Fagerlund and McBride 1975), chinook salmon, *O. tshawytscha*, and catfish, *Ictalurus punctatus* (Higgs et al. 1982). Our addition of MT (1 μg/g) to elver diets significantly increased weight gain and food conversion in all experimental groups, but the strong influence was on M and F fish compared with S fish. Possibly, MT has a different mechanism of action on more mature and therefore, more developed, fish. Androgenic hormones can act by inducing gonadal development. Higgs et al. (1982) reported an increase in the proportion of maturing males treated with 0.5 μg MT/g. McBride and Fagerlund (1973) reported weight gains of 25% above controls after feeding 10 μg MT/g to juvenile coho salmon. When the same species of fish received the same dose in another experiment, the fish gained only 9% above the control during a longer feeding period. The authors suggested that these differences were due to the larger initial size of the fish and the difference in temperature. In our study, the effect of temperature could be partitioned from the effect of size. The decrease in temperature affected growth of elvers differently depending on the initial mean body weight, which was a direct indicator of their growth rate. In S elvers, the temperature drop at day 10 affected both the control and hormone-treated groups (Fig. 1). However, in faster growing elvers the effect of the drop in

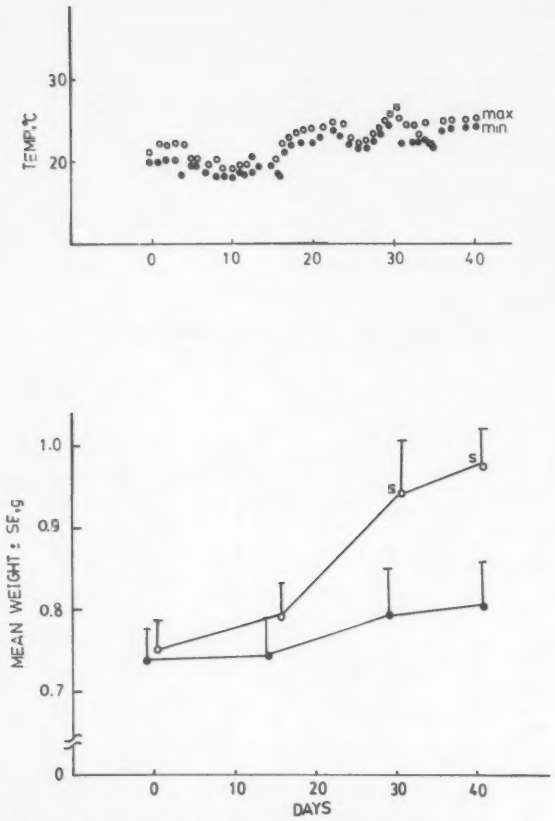


FIG. 4. Changes in mean body weight of M elvers treated with 10 μg bGH/g (○) or untreated controls (●). Superscript *s* indicates a significant difference (*t*-test, $p < 0.05$) between weights of control and treated elvers at a specific time period.

temperature was much more apparent in hormone-treated elvers than in control elvers. Thus, temperature and hormone treatment have different effects in S elvers compared with faster-growing elvers.

Temperature had a significant influence on the growth of both control and treated S elvers. However, with faster-growing elvers, in the presence of hormone that was significantly increasing growth, the effect of decreased temperature was much more pronounced compared with nontreated controls.

bGH significantly accelerated growth of V or M elvers when incorporated into the diet at concentrations of 2 and 10 μg/g, respectively. These data are the first to show the efficiency of dietary growth hormone orally administered to eels. Administration of growth hormone by intramuscular injection is known to enhance fish growth. For example, Kayes (1977) found that bGH increased the growth of *Incalurus melas*. Adelman (1977) demonstrated an increase in growth of carp (*Cyprinus carpia*) when fish were treated with bGH. Higgs et al. (1977) found that bGH enhanced growth in coho salmon to a greater extent than either L-thyroxine ($T_4$) or MT. However, the routine application of bGH by injection is not economical or practical from a management standpoint. In addition, bGH is presently too expensive for routine use. However, if bGH can be successfully incorporated into the diet, it may be useful to add bGH to the diets of small elvers when the total amount of hormone needed would be small.

The effect of temperature on the growth of V elvers receiving bGH was the same as the effect of temperature on growth of control elvers. The relationship between temperature and growth hormone confirmed the results of other studies (Kayes 1977; Adelman 1977). The reduction in temperature has a much stronger influence on growth in S homeothermic elvers than in normally-growing elvers. For this reason, it may not be beneficial to use bGH at temperatures below 23°C.

Both MT- and bGH-treated elvers utilized food more efficiently than controls receiving the same diet without hormone. This agrees with the findings of Fagerlund et al. (1979) that coho salmon fed MT utilized food more efficiently than control groups. However, we found that the effect of bGH on food conversion in V elvers was larger (improvement of 43%) than the effect of MT on slow-developing elvers (improvement of 30%). This result differs from that of Higgs et al. (1977) who found that bGH had a greater influence in growth of yearling coho salmon than did MT. The difference is probably attributable to the size, development, and species of fish.

Total percent body protein was significantly lower in MT-treated (1 μg/g) elvers compared with controls for both M and S elvers (Table 2). Fagerlund et al. (1979) found that the muscle of hormone-treated (1 μg MT/g) coho salmon had slightly lower protein than controls. The percentage of protein apparently is more closely related to the size of the fish than to the hormone treatment.

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## *References*

ADELMAN, I. R. 1977. Effects of bovine growth hormone on growth of carp (*Cyprinus carpio*) and the influences of temperature and photoperiod. J. Fish. Res. Board Can. 34: 509–515.

DEGANI, G., AND D. LEVANON. 1983. The influence of low density on food adaptation, cannibalism and growth of eels (*Anguilla anguilla* (L.)). Bamidgehi, Bull. Fish. Cult. Israel 35: 53–60.

DONALDSON, E. M., U. H. M. FAGERLUND, D. A. HIGGS, AND J. R. MCBRIDE. 1979. Hormonal enhancement of growth in fish, p. 455–597. (W. S. Hoar, D. J. Randall, and J. R. Brett [ed.] Fish physiology. Vol. 8. Academic Press, New York, NY.

FAGERLUND, U. H. M., AND J. R. MCBRIDE. 1975. Growth increments and some fish and gonad characteristics of juvenile coho salmon receiving diets supplemented with 17-α-methyltestosterone. J. Fish. Biol. 7: 305–314.

FAGERLUND, U. H. M., J. R. MCBRIDE, AND E. T. STONE. 1979. A test of 17α-methyltestosterone as a growth promoter in a coho salmon hatchery. Trans. Am. Fish. Soc. 108: 467–472.

GALLAGHER, M. L., E. KANE, AND R. BERINGER. 1984. Effect of size on composition of the American eel, *Anguilla rostrata*. Comp. Biochem. Physiol. A Comp. Physiol. 78: 533–536.

HIGGS, D., E. M. DONALDSON, H. M. DYE, AND J. R. MCBRIDE. 1975. A preliminary investigation of the effect of growth hormone on growth and muscle composition of coho salmon (*Oncorhynchus kisutch*). Gen. Comp. Endocrinol. 27: 240–257.

HIGGS, D. A., U. H. M. FAGERLUND, J. G. EALES, AND J. R. MCBRIDE. 1982. Application of thyroid and steroid hormones as anabolic agents in fish culture. Comp. Biochem. Physiol. B Comp. Biochem. 73: 143–176.

HIGGS , D. A., U. H. M. FAGERLUND, J. R. MCBRIDE, H. M. DYE, AND E. M. DONALDSON. 1977. Influence of combinations of bovine growth hormone, 17α-methyltestosterone and L-thyroxine on growth of yearling coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 55: 1048–1056.

KAYES, T. 1977. Effect of hypophysectomy, beef growth hormone replacement therapy, pituitary autotransplantation, and environmental salinity on

growth in the black bullhead (*Ictalurus melas*). Gen. Comp. Endocrinol. 33: 371–381.

KLEIBER, M. 1975. The fire of life — an introduction of animal energetics. University of California, Robert E. Davis. Krieger Publishing Company, Huntington, NY. 453 p.

LIEWES, E. W. 1978. Eels: bright prospects for farming in Europe. Fish. Farming Int. 5: 8–13.

MCBRIDE, J. R., AND U. H. M. FAGERLUND. 1973. The use of 17α-methyltestosterone for promoting weight increases in juvenile Pacific salomon. J. Fish. Res. Board Can. 30: 1099–1104.

WINDELL, J. T. 1978. Estimating food consumption rates of fish populations, p. 237–238. *In* T. Bagenal [ed.] Methods for assessment of fish production in fresh waters. 3rd ed. Blackwell Scientific Publications Ltd., Oxford, England.

# Size-Selective Feeding by the Predatory Copepod *Epischura lacustris* Forbes

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Wong, C. K., and W. G. Sprules. 1985. Size-selective feeding by the predatory copepod *Epischura lacustris* Forbes. Can. J. Fish. Aquat. Sci. 42: 189–193.

Size-selective predation by *Epischura lacustris* on *Bosmina longirostris* was investigated in the field by comparing the size distributions of *Bosmina* available in the water column with the carapace sizes of killed *Bosmina*. While *Epischura* could consume the entire size range (0.2–0.4 mm) of *Bosmina*, small prey (0.2–0.25 mm) consistently constituted the greatest portion of the diet. For *Bosmina*, vulnerability depended on the rate of encounter with the predator and on the probability of ingestion by the predator. The frequencies of different-sized prey in the diet were partially predicted on the basis of their relative abundance weighted by their ingestion probabilities. The prediction could be improved if encounter rates were known.

Nous avons étudié en milieu naturel la prédation d'*Epischura lacustris* qui chasse *Bosmina longirostris* ; nous avons comparé la distribution des tailles des *Bosmina* vivants de la colonne d'eau avec la longueur de la carapace des sujets tués. *Epischura* mange les *Bosmina* de toutes les tailles (0,2 à 0,4 mm), mais les petits sujets (0,2 à 0,25 mm) représentent la plupart du temps la plus grande partie de son menu. La vulnérabilité de *Bosmina* dépend de la fréquence des rencontres avec le prédateur et de la probabilité que celui-ci l'avale. Nous avons pu déterminer en partie la distribution de fréquences de diverses tailles des proies composant le menu du prédateur d'après leur abondance relative, en pondérant avec les probabilité qu'elles soient avalées. Nos résultats seraient plus précis si nous connaissons la fréquence des rencontres.

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Predatory zooplankters are size-selective, feeding most intensively on small prey (Anderson 1970; Confer 1971; Kerfoot 1977; McQueen 1969). Many models of zooplankton community structure (e.g. Brooks and Dodson 1965; Zaret 1980) are based on the assumption that size-selective predation is the most important ecological force that determines the species composition and size structure of natural communities. Large prey may be less vulnerable to invertebrate predators, but are more visible to planktivorous fish. Optimal body size is thus a compromise among the size-specific rates for foraging, reproduction, and mortality.

Many previous studies of size-selection predation involved experiments carried out in the laboratory where animals were subject to handling and artificial conditions of light and temperature (e.g. Anderson 1970; Confer and Blades 1975; Brandl and Fernando 1978; Wong 1981). Field data have generally been obtained indirectly by documenting changes in the size distribution of the prey animals following a period of exposure to predators in enclosures (Allan 1973; Dodson 1974). Predator gut content analyses provide more direct information on the size of prey eaten (Gophen 1977; Fryer 1957; Murtaugh 1981), but rates of digestion of different prey by different predators are poorly known, and the tendency for predators such as copepods to ingest only part of a prey (Brandl and Fernando 1973; Kerfoot 1978) greatly limits the applicability of this technique.

The calanoid copepod *Epischura lacustris* Forbes preys extensively on and influences the size, life history, and morphology of *Bosmina* spp. (Kerfoot and Peterson 1980). The first objective of this study was to acquire selective feeding data on *Epischura* using a technique that does not suffer many of the deficiencies of the other methods. The technique depends on the fact that *Epischura* ingests only the soft tissue of *Bosmina*, leaving the chitinous carapace that does not decompose readily (e.g. Kerfoot 1974). Assuming that physiological mortality is probably negligible (Hall 1970), the carapace of a killed *Bosmina* is distinguishable from molted exuviae by the presence of broken antennules, various fractures, and remains of soft tissue. A comparison of the size distribution of prey available in the water column with that of the carapaces of killed prey should reveal any pattern of size-selective predation.

A second objective was to determine whether the selective feeding of *Epischura* can be predicted by a model based on the size-dependent vulnerability of prey. For *Bosmina*, the rate of encounter with the predator and the ease of ingestion by the predator are the two major factors determining vulnerability (Wong 1981). Therefore, once the differential encounter and ingestion rates are determined, the proportion of each prey size class ($V_i$) in the diet can be predicted on the basis of prey vulnerability and abundance using the relation

$$V_i = \frac{N_i \cdot E_i \cdot S_i}{\sum_{i=1}^{n} (N_i \cdot E_i \cdot S_i)}$$

where $N_i$, $E_i$, and $S_i$ are the abundance, encounter probability, and ingestion probability, respectively, of prey size class $i$.

## *Materials and Methods*

Field investigations were carried out in Pinks Lake, Quebec, a small meromictic lake with a maximum depth of 20 m. The limnetic zooplankton consisted of *Bosmina longirostris* (O. F. Muller), *Daphnia ambigua* Scourfield, *Daphnia retrocurva* Forbes, *Leptodora kindtii* (Focke), *Diaphanosoma* sp. Fischer, *Diaptomus minutus* Lilljeborg, *Cyclops vernalis* Fischer, *Tropocyclops prasinus mexicanus* Kiefer, and *Epischura lacustris* Forbes. From May to October 1979, zooplankton samples were collected from three sampling stations by duplicate vertical hauls from bottom to surface using a conical plankton net (30.4-cm mouth diameter, 110-μm mesh). The two hauls were combined and preserved in 10% formaldehyde in 500- or 1000-mL bottles. Zooplankton densities at each station were determined by counting subsamples representing 0.02–0.1 of the total sample under a stereomicroscope.

Size-selective predation by *Epischura* was determined by comparing size distributions of killed *Bosmina* with those of *Bosmina* that were alive in the lake. For each sampling date, 100 specimens of each, with at least 25 from each station sampled, were randomly chosen and their length from the front of the head to the base of the mucro was measured at 320× magnification using a compound microscope with an ocular micrometer. Carapaces of different sizes sink through the water column at different speeds, and these were estimated in the laboratory by using a stopwatch to time the sinking speeds of carapaces in a 500-mL glass cylinder (50-mm mouth diameter) containing distilled water at 20°C. Abundances of each of the five size classes of carapaces (the midpoints are 0.2, 0.25, 0.3, 0.35, 0.4 mm) determined from the samples were then corrected for differential sinking rates to obtain unbiased estimates of the size distribution of killed *Bosmina*.

Selectivity for each size class of *Bosmina* was expressed by the standardized forage ratio (SFR) (Chesson 1978; Vanderploeg and Scavia 1979):

$$\frac{r_i/p_i}{\sum_{i=1}^{n} (r_i/p_i)}$$

where $r_i$ is the proportion of killed *Bosmina* in size class $i$ and $p_i$ is the proportion of (formerly) live *Bosmina* in size class $i$. This index gives a measurement of preference that is independent of prey abundance (Paloheimo 1979).

The rate at which *Bosmina* of different sizes will encounter the predator is dependent on the prey swimming speed (Gerritsen and Strickler 1977). To determine the swimming speed of *Bosmina*, 20 animals were placed in a 50-mm-diameter Petri dish containing filtered lake water. Swimming movements were filmed from above with a Sanyo (VC 1600X) video camera fitted with a stereomicroscope lens and recorded with a Gyyr (TLC 200) video recorder. The animals were illuminated from below with a microscope light. The speed of the animals could be determined with 1/30 s resolution (the interframe time) by marking their position on successive frames.

The relationship between ingestion probability, defined as the number of prey killed divided by the number of prey captured, and prey size was determined by presenting *Bosmina* of various sizes to adult *Epischura* in a 50-mm-diameter Petri dish containing filtered lake water. *Epischura*, starved for 24 h, recovered from handling within 2–3 min and started attacking *Bosmina*. A capture was scored if the predator managed to grasp the prey with its mouthparts. Each captured *Bosmina*, whether dead or alive, was removed and sized.

## *Results and Discussion*

Between May and October, *Bosmina* was the most abundant cladoceran herbivore in the zooplankton of Pinks Lake, where it coexisted with three invertebrate predators. The predatory cladoceran *Leptodora kindtii* appeared from late July to the end of August. The number of killed *Bosmina* in the water column, on the other hand, reached a peak in early July (Fig. 1), suggesting that *Leptodora* had little, if any, effect on *Bosmina*. Cyclopoid copepods and the calanoid copepod *Epischura lacustris* existed in Pinks Lake throughout the summer. However, only the density of *Epischura* was correlated with that of killed *Bosmina* ($r = 0.94$, $P < 0.01$) (Fig. 1). There was no significant correlation between the density of cyclopoids and killed *Bosmina* ($r = 0.24$, $P > 0.05$). Furthermore, in contrast with *Epischura*, which scrape the soft tissue out of the carapace, cyclopoid predators ingest *Bosmina* bite by bite and do not leave an intact carapace (Strickler anf Twombly 1975).

These observations suggest that the intact carapaces found in the water column of Pinks Lake during the summer were the result of *Epischura* predation. Thus, the size distribution of killed *Bosmina* reflects the size-selective feeding pattern of *Epischura*. The only contingency that could seriously bias this interpretation and the analysis that follows is differential sinking rates of carapaces of different sizes. In fact, sinking speed of killed *Bosmina* does increase with size (Fig. 2). The 0.25-, 0.3-, 0.35-, and 0.4-mm size classes sink at speeds that are 13.8, 27.5, 41.3, and 55.0% greater, respectively, than that of the 0.2-mm size class. These values were used to adjust the

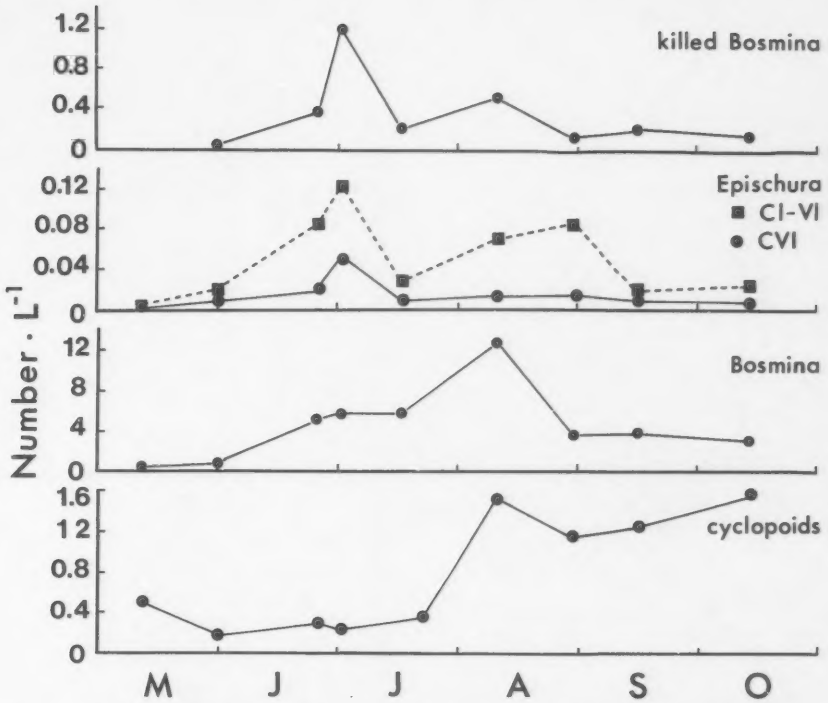


FIG. 1. Densities of *Epischura*, cyclopoid copepods, live *Bosmina*, and killed *Bosmina* in Pinks Lake, 1979. Each point is the mean of three different sampling stations.

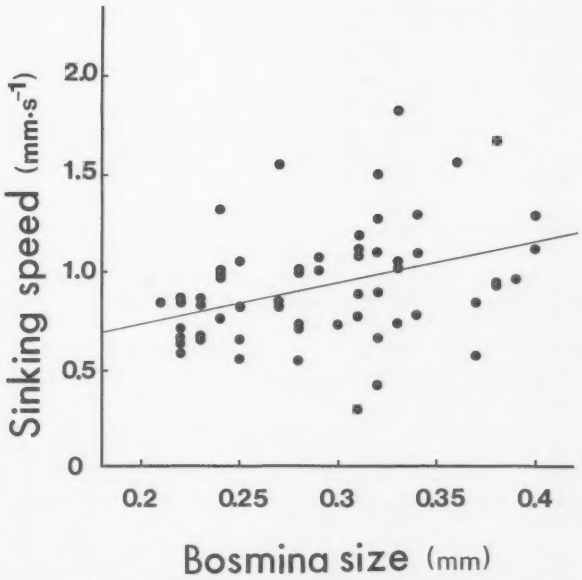


FIG. 2. Sinking speed of *Bosmina* as a function of body size. Each point represents a single animal. Least squares linear regression: speed = 0.34 + 2.06 size. The null hypothesis of a regression coefficient of 0 is rejected at $P < 0.01$ (Student's *t*-test). Thirteen and a half percent of the variance in sinking speed is explained by body size.

abundance of each size class of killed *Bosmina* to obtain an estimate of the size distribution of prey in the diet corrected for differential sinking rate. Resuspension of killed *Bosmina* is unlikely in this meromictic lake, and because our analysis depends only on proportionate (not absolute) abundances of carapaces, their overall sinking rate from the water column is not important.

Using these corrected diet values and the data on *Bosmina* available in the water column, it was possible to compute the pattern of *Epischura* electivity on *Bosmina* (Fig. 3). Although *Epischura* was capable of preying upon the entire size range of *Bosmina* (0.2–0.4 mm), the electivity indices show that the proportion of small prey (0.2 and 0.25 mm) in the diet was higher than would be expected on the basis of their proportion in the lake (Fig. 3).

*Prey vulnerability* — Prey vulnerability depends on encounter rate with the predator and ingestion probability once encountered. The rate at which *Epischura* encounters *Bosmina* of various sizes is influenced by the swimming speed of the prey and the distance from which they can be detected by the predator (Gerritsen and Strickler 1977). Since the swimming speed of *Bosmina* is independent of size ($r = 0.26$, $P > 0.05$), it will not differentially affect encounter rate between *Epischura* and *Bosmina* of varying size. On the other hand, hydromechanical disturbances caused by large *Bosmina* should be greater than those generated by small ones. Since *Epischura* detect prey by sensing these disturbances, large *Bosmina* are probably detected from greater distances and thus experience a higher encounter

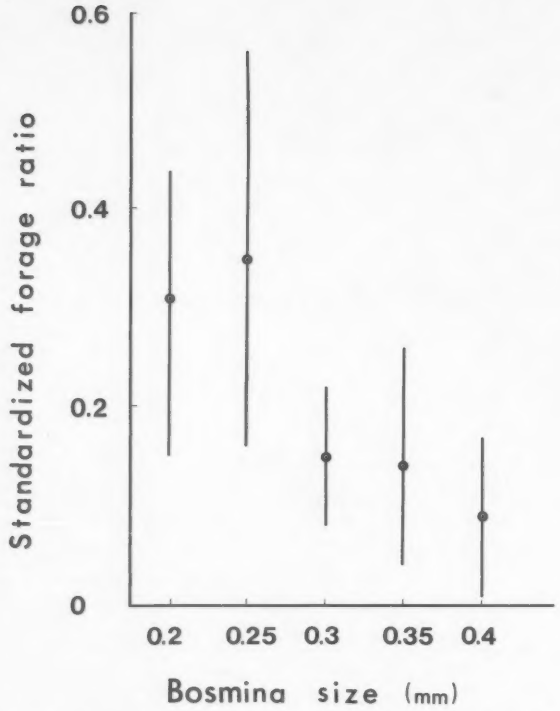


FIG. 3. Size selection by *Epischura* on *Bosmina* of various sizes as expressed by the standardized forage ratio (SFR). Each point is the mean from eight sampling dates; vertical bars represent the range.

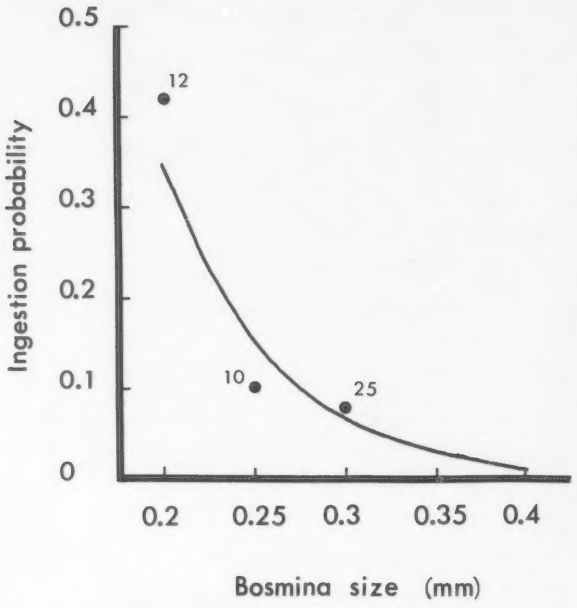


FIG. 4. Ingestion probability as a function of prey body size. Equation of the regression line: ingestion probability = $31.28e^{-19.99\,\text{size}}$.

rate with predators than small *Bosmina*. The exact relationship between encounter probability and prey size is not known because there is no easy way to directly measure the distance from which *Epischura* can detect *Bosmina* of different sizes.

Ingestion probability of *Bosmina*, on the other hand, can be measured directly, and is an inverse function of size (Fig. 4). We never saw *Epischura* successfully ingest *Bosmina* of 0.35 and 0.4 mm, but *Bosmina* of these sizes were preyed upon in the lake (Fig. 3), and occasionally in other laboratory feeding experiments (Wong 1981). Their ingestion probabilities were thus assumed to be higher than zero, and were estimated by extrapolating the curvilinear relationship determined for *Bosmina* 0.2–0.3 mm in size (Fig. 4).

Since the encounter rate between the predator and prey cannot be measured directly, we can estimate its importance indirectly by temporarily ignoring it and computing the vulnerability of the different-sized *Bosmina* by their ingestion probability alone. The first equation thus reduces to

$$V_i = \frac{N_i \cdot S_i}{\sum_{i=1}^{n} (N_i \cdot S_i)}$$

for predicting the size frequency distribution of killed *Bosmina*. The correlation of $r = 0.68$ (Fig. 5, $P < 0.01$) between the observed and predicted frequencies of the various size classes in the diet is moderately strong and indicates that about 46% of the variation in observed frequencies of different-sized prey in the diet can be accounted for by a simple model in which vulnerability is represented by ingestion probability alone. The remaining 54% of variation must, at the very least, be due to inherent variability, predation by the younger instars (our estimates of ingestion probability were based on adult *Epischura*), and variation in encounter probability. The importance of encounter is clear, for the proportion in the diet of large *Bosmina* (which the predator is more likely to detect) is higher than predicted by the simple model (see open triangles and solid circles in Fig. 5), whereas the proportion of smaller *Bosmina* is less than predicted (see solid triangles and squares in Fig. 5). Inclusion of an encounter term in the equation would move points closer to the dotted line (Fig. 5), thus improving the overall power of the model.

The exact relationship between encounter probability and prey size is not known, but could be estimated by plotting the residuals from Fig. 5 against prey size. The relationship is roughly linear, thus supporting Pastorok (1981) who found that the encounter rate between *Daphnia* and *Chaoborus* also increases linearly with prey size.

In conclusion, the result of this study shows that the smallest *Bosmina* are the most vulnerable to the predators. Vulnerability decreases rapidly as a *Bosmina* increases its size from 0.25 to 0.3 mm. Further increases in size result in much smaller decreases in susceptibility. This pattern of differential vulnerability is the result of ingestion probabilities which are determined by the size of a predator's mouthparts and by the manner in which it handles prey (Kerfoot 1978). Laboratory experiments have demonstrated that *Epischura* have low tolerance to starvation (Arts 1983; Wong 1980). Food shortage in the field was indicated by the fact that individuals given extra food in the laboratory quickly increased their weight and lipid content (Arts 1983). Thus, there exists the possibility that food is never abundant enough so that *Epischura* must adopt the opportunistic feeding behavior of attacking all prey encountered. If prey

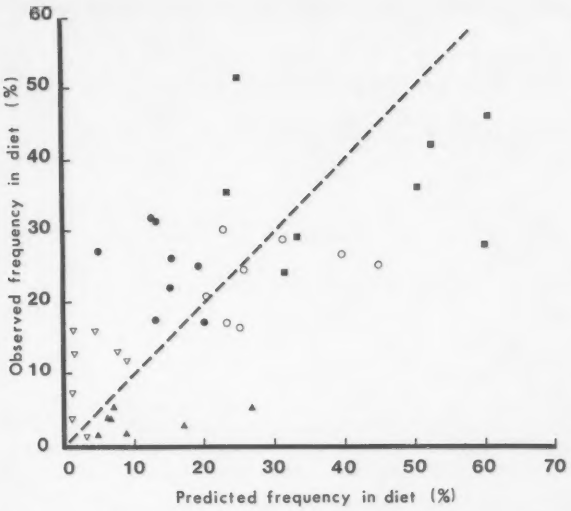


FIG. 5. Correlation between observed and predicted frequencies of different-sized *Bosmina* in the diet of *Epischura*. Each point indicates a particular prey size class on one sampling day. The broken line represents perfect correlation between predicted and observed values. ▲, 0.2 mm; ■, 0.25 mm; ○, 0.3 mm; ●, 0.35 mm; ▽, 0.4 mm.

selection is the result of predator–prey interactions, once the key factors determining the differential vulnerability of prey items are identified and studied, the diet of the predator can be predicted.

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## *References*

ALLAN, J. D. 1973. Competition and the relative abundance of two cladocerans. Ecology 54: 484–498.

ANDERSON, R. S. 1970. Predator–prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. Can. J. Zool. 48: 1229–1240.

ARTS, M. T. 1983. Triacylglycerol energy reserves of *Epischura lacustris* Forbes, *Holopedium gibberum* Zaddach, and *Diaptomus minutus* Lilljeborg (Crustacea) from two lakes with different heavy metal concentrations. M.Sc. thesis, University of Toronto, Toronto, Ont. 79 p.

BRANDL, Z., AND C. H. FERNANDO. 1973. Feeding of the copepod *Acanthocyclops vernalis* on the cladoceran *Ceriodaphnia reticulata* under laboratory conditions. Can. J. Zool. 52: 99–105.

1978. Prey selection by the cyclopoid copepods *Mesocyclops edax* and *Cyclops vicinus*. Verh. Int. Ver. Limnol. 20: 2505–2510.

BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. Science (Wash., DC) 150: 28–35.

CHESSON, J. 1978. Measuring preference in selective predation. Ecology 59: 211–215.

CONFER, J. L. 1971. Intrazooplankton predation by *Mesocyclops edax* at natural prey densities. Limnol. Oceanogr. 15: 663–666.

CONFER, J. L., AND P. I. BLADES. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20: 571–579.

DODSON, S. I. 1974. Zooplankton competition and predation: an experimental test of the size efficiency hypothesis. Ecology 55: 605–613.

FRYER, G. 1957. The food of some freshwater cyclopoid copepods and its ecological significance. J. Anim. Ecol. 26: 263–286.

GERRITSEN, J., AND J. R. STRICKLER. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. 34: 73–82.

GOPHEN, M. 1977. Food and feeding habits of *Mesocyclops leuckarti* (Claus) in Lake Kinneret (Israel). Freshwater Biol. 7: 513–518.

HALL, D. J. 1970. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. Ecology 45: 94–112.

KERFOOT, W. C. 1974. Net accumulation rates and the history of cladoceran communities. Ecology 55: 51–61.

1977. Implications of copepod predation. Limnol. Oceanogr. 22: 316–325.

1978. Combat between predatory copepods and their prey: *Cyclops*, *Epischura*, and *Bosmina*. Limnol. Oceanogr. 23: 1089–1102.

KERFOOT, W. C., AND C. PETERSON. 1980. Predatory copepods and *Bosmina*: replacement cycles and the further influences of predation upon prey reproduction. Ecology 61: 417–431.

MCQUEEN, D. J. 1969. Reduction of zooplankton standing stocks by predaceous *Cyclops bicuspidatus thomasi* in Marion Lake, British Columbia. J. Fish. Res. Board Can. 26: 1605–1618.

MURTAUGH, P. A. 1981. Selective predation by *Neomysis mercedis* in Lake Washington. Limnol. Oceanogr. 26: 445–453.

PALOHEIMO, J. E. 1979. Indices of food preference by a predator. J. Fish. Res. Board Can. 36: 470–473.

PASTOROK, R. A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. Ecology 62: 1311–1324.

STRICKLER, J. R., AND S. TWOMBLY. 1975. Reynolds number, diapause, and predatory copepods. Verh. Int. Ver. Limnol. 19: 2943–2950.

VANDERPLOEG, H. A., AND D. SCAVIA. 1979. Two electivity indices for feeding with special reference to zooplankton grazing. J. Fish. Res. Board Can. 36: 362–365.

WONG, C. K. 1980. Copepod predation and prey defense. M.Sc. thesis, University of Ottawa, Ottawa, Ont.

1981. Predatory feeding behavior of *Epischura lacustris* (Copepoda, Calanoida) and prey defense. Can. J. Fish. Aquat. Sci. 38: 275–279.

ZARET, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, CT.

# The Uncertain Influence of Spring Photoperiod on Spawning in the American Lobster, *Homarus americanus*

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Aiken, D. E., and S. L. Waddy. 1985. The uncertain influence of spring photoperiod on spawning in the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 194–197.

The literature contains a report that induction of final vitellogenesis and time of spawning in American lobsters (*Homarus americanus*) is controlled by spring photoperiod. However, we could not corroborate this. Two experiments with American lobsters held throughout the winter in Canadian Atlantic seawater temperatures indicated no effect of spring photoperiod on time of spawning. In one experiment the onset of spring photophase was delayed by 2 mo. In the second experiment the photophase at the winter solstice (9 h 46 min) was gradually shortened over ensuing months to 5 h 30 min on 7 July. Neither of these treatments altered the time of spawning relative to control animals on a simulated natural photoperiod cycle. Spawning occurred at photoperiods of LD 6:18 and LD 15:9.

Il est signalé dans les communications que l'induction de la vitellogenèse définitive et du moment du frai chez le homard d'Amérique (*Homarus americanus*) est régie par la photopériode de printemps. Nous n'avons cependant pu vérifier ce phénomène. Deux expériences portant sur des homards d'Amérique conservés tout au long de l'hiver aux températures de l'eau de mer de l'Atlantique canadien n'ont permis de déceler aucun effet de la photopériode de printemps sur le moment du frai. Dans l'une des expériences, le début de la photophase de printemps a été retardé de deux mois. Dans l'autre, la photophase du solstice d'hiver (9 h 46 min) a été graduellement raccourcie au cours des mois suivants jusqu'à la valeur de 5 h 30 min au 7 juillet. Aucun de ces traitements n'a déplacé le moment du frai par rapport à celui d'animaux témoins soumis à un cycle naturel de photopériode simulé. Le frai s'est produit aux photopériodes (E:O) de 6:18 et de 15:9.

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Photoperiod has been shown to play an important role in the regulation of short- and long-term reproductive cycles and in the timing of molting and oviposition in decapods and other marine organisms (Paris and Jenner 1952; Stephens 1952; Lowe 1961; Aiken 1969a, 1969b; Perryman 1969; Segal 1970; Rice and Armitage 1974; Quackenbush and Herrnkind 1983).

In a given stock and reproductive class of wild American lobsters (*Homarus americanus*), spawning occurs at roughly the same time in individuals, and this synchrony can be maintained for years in the laboratory by simulating natural cycles of temperature and photoperiod (Waddy and Aiken 1984a). Recently, Nelson et al. (1983) reported that spring photoperiod controls spawning in American lobsters. They found that a change in photoperiod from LD 8:16 to LD 16:8 initiated a 100–120 d period during which the events leading to egg extrusion could be initiated.

Nelson et al. (1983) used lobsters obtained on the Atlantic coast (Massachusetts) and transported 5000 km west to the Pacific coast (California). The subsequent molting and reproductive events that Nelson et al. (1983) obtained from these animals were not what our earlier work would lead us to expect from mature female lobsters in Atlantic waters (Aiken and Waddy 1982), an indication that the unusually warm winter water temperature of the central California coast may have altered their physiological responses. This is an important concern because the results reported by Nelson et al. (1983) are being cited by others (Hedgecock et al. 1983; Malecha 1983; Van Olst et al. 1980) and have been incorporated into a technique for controlling lobster breeding under culture conditions (Hedgecock 1983). It is therefore important to know that the biological principles brought out by Nelson et al. (1983) are not peculiar to the environmental conditions of the California coast.

To assess this we conducted two separate experiments with mature female American lobsters on the Atlantic coast of Canada. These experiments were not intended to duplicate the experiments of Nelson et al. (1983), but rather to apply the principles established by them in their original study and expanded upon in subsequent publications (e.g. Hedgecock 1983).

## *Methods*

*Lobsters* — Mature female lobsters 73–80 mm CL with an abdomen width to carapace length ratio of at least 0.67 were obtained in autumn from the commercial fishery at Miminegash, Prince Edward Island (southern Gulf of St. Lawrence, 47°N). Females were held in communal tanks, with shelter, in local seawater temperature and photoperiod until 21 December. All females used in experiments had cement glands at development stage 1.0 or greater, indicating that they were physiologi-

cally capable of spawning in the next reproductive season (Aiken and Waddy 1982).

*Holding conditions* — Lobsters were fed daily on a rotation of fish, squid, shrimp, or beef liver, with occasional supplements of rockweed (*Fucus*). Control and experimental animals were held individually in identical fiberglass tanks. Individual cubicles in these tanks were 23 × 39 × 41 cm deep with a water depth of 34 cm. Seawater of 31‰ average salinity was filtered through sand and supplied to each cubicle at 0.4 L/min. Tanks were in a light-proof cabinet in which illumination supplied by incandescent lamps averaged 22 lm/$m^2$ at the surface. Photoperiod was controlled by General Electric TSA-47 time clocks, reset on Monday of each week. Daylength was obtained from tables for Saint John, New Brunswick (approximately 45°N). The photophase included 30 min before sunrise and after sunset (civil twilight, sun approximately 6° below the horizon).

*Experiment 1: Delayed spring photoperiod* — Eighteen experimental and 18 control females were transferred to the photoperiod tanks on 21 December, when the photophase in the control tank began to increase at the normal postsolstice rate (Fig. 1A). The photophase in the experimental tank was held at 9 h 46 min (21 December photoperiod) until 21 February, when it also began increasing at the normal postsolstice rate (Fig. 1B). Experimental animals therefore were 60 d behind the controls in attaining the same "spring" photoperiod. On 7 July the photophase in the experimental group was 15 h 30 min versus 16 h 30 min for the control group. Water temperature was the same for each group and varied as the seawater temperature in the St. Croix estuary on Passamaquoddy Bay (Fig. 2). Females were examined daily for cement gland development, evidence of ovary resorption, and egg extrusion.

*Experiment 2: Decreasing spring photophase* — Eighteen experimental and 19 control females were transferred to the photoperiod tanks on 21 December. Photophase in the control tank was increased at the normal postsolstice rate. Photophase in the experimental tank decreased gradually through spring and summer (Fig. 1C). By 7 July the photophase in the experimental group was 5 h 30 min versus 16 h 30 min in the control group.

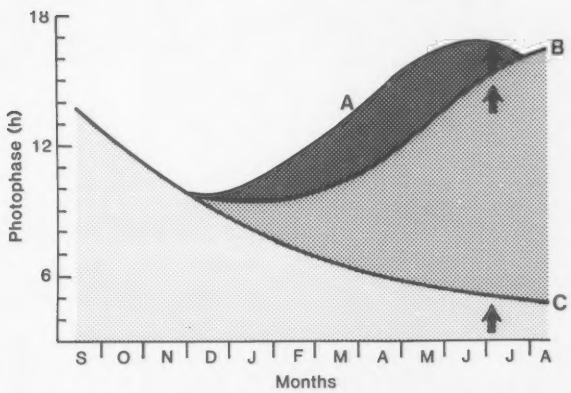


FIG. 1. Effect of different "spring" photoperiods on spawning in the American lobster. A, control photoperiod based on local civil twilight; B, onset of spring photoperiod delayed by 2 mo (photophase held constant from 21 December through 21 February); C, progressive decrease in length of photophase throughout spring and summer. Time of spawning in each treatment indicated by arrows.

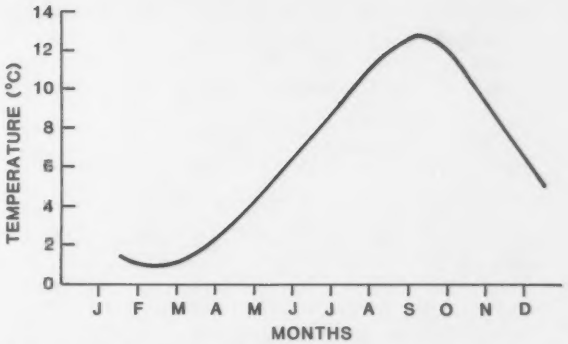


FIG. 2. Annual seawater temperature at St. Andrews, New Brunswick. Plotted from average temperature on the 15th of each month over a 4-yr period.

Water temperature was the same for each group (Fig. 2). As in experiment 1, females were examined daily.

## *Results*

*Experiment 1: Delayed spring photoperiod* — The ovaries of 1 control and 2 experimental females were resorbed (dark green hemolymph visible through the sternal membrane of abdomen) and the other 33 females spawned. Mean calendar day of extrusion was 193 for controls and 200 for experimentals (Table 1).

*Experiment 2: Decreasing spring photophase* — Ovaries of 1 control and 1 experimental female were resorbed and the other 35 females spawned. Mean calendar day of extrusion was 193 for controls and 196 for experimentals (Table 1).

Student–Neumann–Kuels ranked analysis of variance showed no significant difference ($\alpha = 0.05$) in mean day of extrusion for any of the four groups in these two experiments.

## *Discussion*

Hedgecock (1983), applying the principles developed in his work with Nelson and Borgeson, wrote:

> ... an artificial extension of winter lighting conditions allows the scheduling of egg laying for the otherwise barren months of late fall and winter. ...

In experiment 1 we extended the winter lighting conditions by 60 d but obtained no comparable delay in extrusions by experimental animals. We conclude that the extension of winter lighting conditions had no inhibitory effect on vitellogenesis and spawning under the conditions of this experiment.

Hedgecock (1983) also speculated that the vernal equinox is the natural photoperiod trigger for egg laying in midsummer. Lobsters in experiment 2 did not experience a photoperiod equivalent to the vernal equinox. In fact, at the time of the vernal equinox the photophase was only 6.5 h long and decreasing, yet this group spawned at the same time as the control females. This response indicates a lack of sensitivity to direction of change as well as to absolute length of the photophase (or scotophase).

These two experiments provide no evidence that spring photoperiod is involved in the control of spawning in American lobsters, and no evidence in support of observations by Nelson et al. (1983). Our experiments were not a duplication of their study and there were several important differences in methodology. Most significant were the stock of lobsters and the differences in temperature and photoperiod regimes.

TABLE 1. Day of egg extrusion by control and experimental females under different "spring" photoperiods.

| | Experiment 1 | | Experiment 2 | |
|---|---|---|---|---|
| | Control | Delayed photoperiod | Control | Decreasing photoperiod |
| Day | 193 | 200 | 193 | 196 |
| SD | 8.1 | 8.0 | 7.9 | 8.2 |
| Group *N* | 18 | 18 | 19 | 18 |
| Spawning *N* | 17 | 16 | 18 | 17 |

Our experimental animals were obtained from the southern Gulf of St. Lawrence (approximately 47°N). Those of Nelson et al. (1983) were taken from the New England coast at approximately 42°N. It seems unlikely that this could account for such a pronounced difference in the response of the reproductive system to spring photoperiod, especially since lobsters at the Massachusetts State Lobster Hatchery spawn at roughly the same time as those held in our laboratory.

In our experiments a progressively changing photoperiod was used and the minimum winter photophase was 9 h 46 min. Nelson et al. (1983) used a constant photoperiod with an abrupt change from LD 8:16 to LD 16:8. Their minimum winter photophase of 8 h was 1 h 46 min shorter than ours. Was our winter photophase too long to permit a proper response to summer photoperiod? The evidence suggests not, for two reasons. First, we obtained spawning from 95% of experimental animals with a high degree of synchrony. This was a much better spawning percentage and degree of synchrony than was obtained by Nelson et al. (1983). Second, their lobsters were obtained from Martha's Vineyard, Massachusetts, on 20 December. Photophase at that time was more than 9 h (10 h if twilight is included). Hedgecock (1983) noted that lobsters routinely extrude in the ambient photoperiod at the Massachusetts State Lobster Hatchery, and the photoperiod there is little different from that used in our experiments.

The temperature regimes experienced by lobsters in the two studies were dramatically different. Winter temperature in their study did not drop below approximately 10°C, whereas the winter temperature in our study remained below 5°C for 4 mo. If temperature accounts for the difference in response in the two studies, it suggests that lobsters that do not utilize photoperiod in their natural Atlantic environment are nevertheless capable of doing so if transferred to a location with warmer winter water temperatures.

In earlier studies we found that a period of winter temperature below 5°C was necessary to maintain reproductive synchrony among individuals and to maintain a proper relationship between the molting and reproductive cycles of an individual (Waddy and Aiken 1984b). When water temperature remained above 9–10°C throughout the winter (as it did in the experiments of Nelson et al. 1983) we found that the molting cycle began to dominate at the expense of the reproductive cycle. Extra molts occurred, incidence of ovary resorption increased, and the reproductive cycles of females became individualistic (Waddy and Aiken 1984a, 1984b). These are also the responses obtained by Nelson et al. (1983) at Bodega Bay.

An inordinate number of the females maintained by Nelson et al. (1983) either molted and then molted again, or molted and then extruded shortly thereafter. Both situations are unusual for mature females in their natural environment. In some areas, approximately 20% of the females entering their first spawning cycle will molt and spawn shortly thereafter, but Nelson et al. (1983) obtained this molt–extrude cycle in 71% of their spawning females. The extrude–hatch–molt response is by far the most common for mature females in the wild (Aiken and Waddy 1982), but it occurred in fewer than 20% of the females in their study. To us this suggests that their experimental animals may have included some immature and maturing females as well.

Other information supports this assumption. Nelson et al. (1983) used females with an abdomen width to carapace length ratio of only 0.62. We have found that as few as 50% may be mature at a ratio of 0.65, and that a ratio of 0.67 must be used if a high percentage of maturity is essential (Waddy and Aiken 1980). The presence of immature and maturing lobsters would not in itself cause a photoperiod effect to be indicated where none existed, but it would increase the variability in responses to experimental conditions and thereby increase the possibility of misleading statistical interpretation (Aiken and Waddy 1985).

In summary, our two experiments have indicated no relationship between spring photoperiod and the timing of egg laying in wild American lobsters maintained on a winter temperature cycle typical of Canadian Atlantic nearshore waters. These results contrast with those of Nelson et al. (1983), who found a pronounced effect of spring photoperiod on wild American lobsters maintained in different photoperiod and temperature conditions on the central California coast. It therefore appears that the role of spring photoperiod in the control of spawning is not as well defined as the current literature indicates.

*Acknowledgments*

We thank D. W. McLeese and A. Campbell for valuable comments on the manuscript.

*References*

AIKEN, D. E. 1969a. Photoperiod, endocrinology, and the crustacean molt cycle. Science (Wash., DC) 164: 149–155.

1969b. Ovarian maturation and egg laying in the crayfish *Orconectes virilis*: influence of temperature and photoperiod. Can. J. Zool. 47: 931–935.

AIKEN, D. E., AND S. L. WADDY. 1982. Cement gland development, ovary maturation and reproductive cycles of female American lobsters, *Homarus americanus*. J. Crustacean Biol. 2: 315–327.

1985. Photoperiodic control of vitellogenesis in the American lobster (*Homarus americanus*): comment on a recent report. Can. J. Fish. Aquat. Sci. 42: 198–199.

HEDGECOCK, D. 1983. Maturation and spawning of the American lobster, *Homarus americanus*, p. 261–270. *In* J. P. McVey [ed.] CRC handbook of mariculture. Vol. 1. Crustacean aquaculture. CRC Press, Boca Raton, FL.

HEDGECOCK, D., M. L. TRACY, AND K. NELSON. 1983. Genetics, p. 283–403. *In* L. G. Abele [ed.] The biology of crustacea. Vol. 2. Embryology, morphology and genetics, Academic Press, New York, NY.

LOWE, M. E. 1961. The female reproductive cycle of the crayfish, *Cambarellus shufeldti*: the influence of environmental factors. Tulane Stud. Zool. 8: 157–176.

MALECHA, S. R. 1983. Crustacean genetics and breeding: an overview. Aquaculture 33: 395–413.

NELSON, K., D. HEDGECOCK, AND W. BORGESON. 1983. Photoperiodic and ecdysial control of vitellogenesis in lobsters (*Homarus*) (Decapoda, Nephropidae). Can. J. Fish. Aquat. Sci. 40: 940–947.

PARIS, O. H., AND C. E. JENNER. 1952. Photoperiodism in the fresh water shrimp, *Palaemonetes paludosus* (Gibbes). J. Elisha Mitchell Sci. Soc. 68: 144.

PERRYMAN, E. K. 1969. *Procambarus simulans*: light induced changes in neurosecretory cells and in ovarian cycle. Trans. Am. Microsc. Soc. 8: 514–524.

QUACKENBUSH, L. S., AND W. F. HERRNKIND. 1983. Regulation of the molt

cycle of the spiny lobster, *Panulirus argus*: effect of photoperiod. Comp. Biochem. Physiol. 76A: 259–263.

RICE, P. R., AND K. B. ARMITAGE. 1974. The influence of photoperiod on processes associated with molting and reproduction in the crayfish *Orconectes nais* (Faxon). Comp. Biochem. Physiol. 47A: 243–259.

SEGAL, E. 1970. Light, invertebrates, p. 159–211. *In* O. Kinne [ed.] Marine biology, Wiley-Interscience, London.

STEPHENS, G. J. 1952. Mechanisms regulating the reproductive cycle in the crayfish *Cambarus*.. 1. The female cycle. Physiol. Zool. 25: 70–84.

VAN OLST, J. C., J. M. CARLBERG, AND J. T. HUGHES. 1980. Aquaculture, p. 333–384. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters, Vol. 2. Academic Press, New York, NY.

WADDY, S. L., AND D. E. AIKEN. 1980. Abdomen width and carapace length, a maturity index for female lobsters, *Homarus americanus*. CAFSAC Res. Doc. 80/40: 11 p. (Available from Library, Biological Station, St. Andrews, N.B. E0G 2X0)

1984a. Broodstock management for continuous production of larvae for lobster culture. Can. Tech. Rep. Fish. Aquat. Sci. 1272: 14 p.

1984b. Environmental regulation of ovarian development in the American lobster (abstract), p. 649. *In* W. Engles, W. H. Clark Jr., A. Fischer, P. J. W. Olive, and D. F. Went [ed.] Advances in invertebrate reproduction 3. Elsevier Science Publishers, Amsterdam.

# LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

## Photoperiodic Control of Vitellogenesis in the American Lobster (*Homarus americanus*): Comment on a Recent Report

According to Nelson et al. (1983), events leading to egg extrusion in *Homarus americanus* are related to long-day photoperiod in spring. If true, this would be a significant advance in our understanding of lobster reproduction, and as Hedgecock (1983) has pointed out, it would simplify the breeding of cultured American lobsters.

Unfortunately, we are skeptical that long days in spring initiate "... a period of 100–120 d during which the events leading to egg extrusion may be initiated ..." or that a female that fails to enter or complete vitellogenesis during the summer "... must await the stimulus of LDO the following spring for another chance." Our own experiences with this animal indicate that spring photoperiod has no such effect in the natural environment (Aiken and Waddy 1985).

Nelson et al. (1983) used wild, presumably mature females from Martha's Vineyard in Massachusetts. They were transported to California in December and held at ambient temperature (14°C) under short-day photoperiod (LD 8:16). At 28-d intervals in April, May, and June, groups of these females were transferred to long-day photoperiod (LD 16:8). The results, summarized on line 4 of their table 1, show that spawning occurred in each group 140–148 d after exposure to long-day photoperiod (LDO), irrespective of the date of LDO. This appears to be good evidence for photoperiodic regulation of events leading to spawning.

However, if females from Martha's Vineyard are like females from Canadian waters, spring photoperiod has little effect on the induction of vitellogenesis and spawning, and spawning cannot be prevented or delayed by simply extending the winter photoperiod into the spring and summer. We suspect the results reported by Nelson et al. (1983) are an artifact of the water temperature at Bodega Bay and their method of data analysis. For example, the value on line 4 of their table 1 (time from LDO to extrusion) are an amalgam of two types of reproductive response: females that responded to LDO by spawning and females that responded to LDO by first molting and then spawning. When two groups respond differently to the same environmental stimulus, there is reason to suspect that they are physiologically dissimilar and should not be combined for statistical analysis.

Under environmental conditions encountered in the natural range of this species the rule is for a female to either molt or spawn in a given summer. The exception to this rule is the Adult I reproductive class (maturing for the first time), in which up to 20% may molt and spawn in the same summer (Aiken and Waddy 1980, 1982; Ennis 1980; Robinson 1979). The percentage of these Adult I females that molt and then spawn appears to be linked to summer temperature. Adult I females that molt before spawning perforce spawn later in the season and are, because of the impact of molting on reproductive physiology, different from their Adult II and Adult III counterparts.

However, when the data of Nelson et al. (1983) are separated into those that molted before spawning (their MEM group) and those that spawned without molting (their EM group), the picture becomes less clear. Group EM, the best group to analyze because there is no interference from the molt cycle, comprises only 29% (10/34) of the total number of spawners and is difficult to handle because of small numbers in each treatment ($N$ = 1, 4, 5) and the large within-treatment variation in time from LDO to spawning. Group MEM, on the other hand, which constituted 71% (21/34) of the total number of spawning females, had larger sample sizes but an excessive difference in time from LDO to spawning. Neither of these groups was analyzed separately by Nelson et al. (1983). Instead the two groups were combined and subjected to one-way ANOVA of extrusion dates that, because of the effect of pooling, appear to be similar (e.g. in the third treatment group, $N$ = 10 overpowers $N$ = 1). In addition, there appear to be conflicting statements on the effect of LDO on an extrusion that follows a molt (see p. 942 and 944), and the complication that arises when spawning dates are grouped weekly (e.g. two females spawning 7 d apart can be recorded on the same day, and two females spawning on the same day can be recorded 7 d apart).

We feel the normal physiological responses of the lobsters used by Nelson et al. (1983) were confounded by the abnormally high winter water temperature of the central California coast. We also suspect that their interpretation of experimental results was confounded by the presence of immature and maturing females among the experimental animals, the practice of recording extrusions on a weekly basis, and the combining of two or more different reproductive responses into a single group for analysis. We would be more comfortable with the conclusions reached by Nelson et al. (1983) if they were supported by a second study in which some of these uncertainties were removed — D. E. Aiken and S. L. Waddy, *Department of Fisheries and Oceans, Fisheries and Environmental Sciences, Fisheries Research Branch, Biological Station, St. Andrews, N.B. E0G 2X0.*

### *References*

AIKEN, D. E., AND S. L. WADDY. 1980. Reproductive biology, p. 215–276. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

1982. Cement gland development, ovary maturation and reproductive cycles of female American lobsters, *Homarus americanus*. J. Crustacean Biol. 2: 315–327.

1985. The uncertain influence of spring photoperiod on spawning in the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 194–197.

ENNIS, G. P. 1980. Size–maturity relationships and related observations in Newfoundland populations of the lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 37: 945–956.

HEDGECOCK, D. 1983. Maturation and spawning of the American lobster, *Homarus americanus*, p. 261–270. *In* J. P. McVey [ed.] CRC handbook

of mariculture, Vol. 1. Crustacean aquaculture. CRC Press, Boca Raton, FL.

NELSON, K., D. HEDGECOCK, AND W. BORGESON. 1983. Photoperiodic and ecdysial control of vitellogenesis in lobsters (*Homarus*) (Decapoda, Nephropidae). Can. J. Fish. Aquat. Sci. 40: 940–947.

ROBINSON, D. G. 1979. Consideration of the lobster (*Homarus americanus*) recruitment overfishing hypothesis, with special reference to the Canso causeway. Can. Fish. Mar. Serv. Tech. Rep. 834: 77–99.

## Reply to Aiken and Waddy

Aiken and Waddy (1985b) question the results and interpretation of our study of the interaction of photoperiod and the molt cycle in timing egg extrusion in the American lobster (*Homarus amaricanus*) (Nelson et al. 1983). We reported that under our laboratory conditions, females from Martha's Vineyard (Massachusetts) required a period of short days to prepare for final vitellogenesis, and that extrusion occurred approximately 120 d following the resumption of long days (LDO). However, if molting intervened between 40 and 120 d following LDO, extrusion was postponed approximately 80 d; if molting was due to occur after 120 d post-LDO, extrusion was not seen at all.

They state that we combined the data from those females that molt prior to extrusion (group MEM in our paper) and those that did not (group EM): "Neither of these groups was analyzed separately by Nelson et al. (1983). Instead the two groups were combined and subjected to one-way ANOVA of extrusion dates ..." This is hardly a fair description of our analysis. We spent several paragraphs (Nelson et al. 1983, p. 942–944) elucidating the differences between groups EM and MEM, and while it is true that we did not present a separate ANOVA for group EM dates of extrusion, we most certainly did so for group MEM (p. 944; $F = 5.30$; df 2,21; $p < 0.02$). For the record, an ANOVA of EM extrusion dates for the three photoperiod conditions is also significant ($F = 5.720$; df 2,7; $p < 0.05$).

They also suggest that our results are an artifact of weekly sampling. Even in the most extreme case the maximum resulting error in mean extrusion date would be less than 7 d. Thus, it is impossible that our weekly sampling could have produced the ranges in mean extrusion date which we found in different photoperiod conditions (all extrusions, 54 d, group EM, 51 d; group MEM, 36 d; see our table 1). They also suggest that our interpretation may have been confounded by the presence of immature individuals. We carefully selected females on the basis of *four restrictive criteria*, including a serum concentration of vitellogenin of at least 0.2 mg/mL (not just on the basis of a ratio of abdomen width to carapace length of greater than 0.62 as stated in Aiken and Waddy 1985a). In any event, as lobsters were randomly assigned to photoperiod treatments, immature animals would presumably have increased the percentage in each treatment group that did *not* spawn. Beyond that, we wish that Aiken and Waddy had been more explicit in telling of the effect they imagine.

Aiken and Waddy neglect the results we presented of our earlier (unpublished) experiments, all of which support our photoperiodic interpretation. In summary, for 75 extruding animals from Martha's Vineyard which experienced short days beginning in the fall and ending variously on days 026, 073, 108, 136, 164, and 240 of the following year, the regression of date of extrusion on date of LDO was $y = 138.4 + 1.012x$, with a coefficient of determination ($r^2$) of 0.889 (Nelson et al. 1983, fig. 5 and caption). In other words, on the average, a delay in LDO of 1 d results in a delay in extrusion of 1 d.

All the above LDO groups contained varying numbers of EM and MEM animals, depending upon the phase of LDO in an individual's molt cycle. The experiment questioned by Aiken and Waddy was *explicitly* concerned with elucidating the effects of the molt in delaying or eliminating extrusion and with the apparent paradox (their "conflicting statements"?) that, while LDO did not affect date of molt generally, it seemed to do so if the molt was to be followed by an extrusion.

We have subsequently used the technique of photoperiodic induction to study further the interaction of the molt and reproductive cycles in successive molt cycles of more than 100 individuals. These later results modify our earlier conclusions only by extending the post-LDO period in which an impending molt abolishes an extrusion.

As we discussed at length in our paper, we agree with Aiken and Waddy that "the normal physiological responses (of our lobsters) were confounded by the abnormally high winter water temperatures of the central California coast." This does not invalidate our results, but as we again discussed at length, it affects their application to the field situation. We cited Aiken and Waddy (1976) and D. E. Aiken (pers. comm.) on the suppression of, respectively, molting and vitellogenesis by low winter temperatures, and agree with them that this probably prevented in the field much of the conflict we observed in the laboratory. But this says nothing about whether photoperiod is or is not the operative cue for vitellogenesis in nature.

In their comment, Aiken and Waddy state that "if females from Martha's Vineyard are like females from Canadian waters, spring photoperiod has little effect on the induction of vitellogenesis and spawning, and spawning cannot be prevented or delayed by simply extending the winter photoperiod into the spring and summer." By "Canadian" lobsters they mean specifically those from the vicinity of Prince Edward Island in the Gulf of St. Lawrence, with which all of their photoperiod and temperature studies have dealt exclusively (S. L. Waddy, pers. comm.). From a published abstract (Waddy and Aiken 1984) we may gather that they consider temperature increase in the spring to provide the cue for final vitellogenesis in these animals, although it is evident that they have not confirmed this experimentally (Aiken and Waddy 1985a).

Although in a pilot experiment with Martha's Vineyard animals ("groups A1–4" in Nelson et al. 1983, fig. 5) we found no effect of differences in duration or timing of a 6°C cold period upon the date of extrusion, we acknowledge that temperature change might well be the operative stimulus in Prince Edward Island animals. Preliminary results from a group of the same stock kindly sent to us by Susan Waddy are compatible with a role for temperature in inducing extrusion.

We earlier found electrophoretic evidence of substantial geographic isolation between Prince Edward Island and Massachusetts lobsters, in the form of a fixed difference at one locus (Tracey et al. 1975). (This result has been criticized by Shaklee (1983); and although we disagree with the basis of Shaklee's main objection, we agree that this observation needs to be replicated.) If so, a genetic difference may well exist between the populations in their reproductive responses to environmental cues. There may be no conflict after all between the results of our several experiments and the results of Aiken and Waddy (1985a). It is also quite possible given the data now available that under different circumstances in the two populations, a photoperiodic response may be modified by prevailing temperature or vice versa, producing the disparate effects that we see. Such interactions are not unusual, for example in the control of

the timing of diapause in insects and copepods (Beck 1980; Marcus 1984) — K. Nelson and D. Hedgecock, *Bodega Marine Laboratory, University of California, Bodega Bay, CA 94923, USA*.

### *References*


AIKEN, D. E., AND S. L. WADDY. 1976. Controlling growth and reproduction in the American lobster. Proc. World Maricult. Soc. 7: 415–430.

1985a. The uncertain influence of spring photoperiod on spawning in the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 194–197.

1985b. Photoperiodic control of vitellogenesis in the American lobster (*Homarus americanus*): comment on a recent report. Can. J. Fish. Aquat. Sci. 42: 198–199.

BECK, S. D. 1980. Insect photoperiodism. 2nd ed. Academic Press, New York, NY.

MARCUS, N. 1984. Variation in the diapause response of *Labidocera aestiva* (Copepoda: Calanoida) from different latitudes and its importance in the evolutionary process. Biol. Bull. 166: 127–139.

NELSON, K., D. HEDGECOCK, AND W. BORGESON. 1983. Photoperiodic and ecdysial control of vitellogenesis in lobsters (*Homarus*) (Decapoda, Nephropidae). Can. J. Fish. Aquat. Sci. 40: 940–947.

SHAKLEE, J. B. 1983. The utilization of isozymes as gene markers in fisheries management and conservation. Isozymes Curr. Top. Biol. Med. Res. 11: 213–247.

TRACEY, M. L., K. NELSON, D. HEDGECOCK, R. A. SHLESER, AND M. L. PRESSICK. 1975. Biochemical genetics of lobsters: genetic variation and the structure of American lobster (*Homarus americanus*) populations. J. Fish. Res. Board Can. 32: 2091–2101.

WADDY, S. L., AND D. E. AIKEN. 1984. Environmental regulation of ovarian development in the American lobster (abstract), p. 649. *In* W. Engels, W. H. Clark Jr., A. Fischer, P. J. W. Olive, and D. F. Went [ed.] Advances in invertebrate reproduction 3. Elsevier Science Publishers, Amsterdam.

# BOOK REVIEWS/COMPTES RENDUS

**The Ecology of Aquatic Insects** *Edited by V. H. Resh and D. M. Rosenberg. Praeger Publishers, New York, NY. 1984. 625 p.*

On first reading of the chapter titles, the only obvious subjects missing from the book are (1) those aquatic habitats that include estuaries, brackish water, saline lakes, and intertidal zones, (2) ecology of aquatic insects inhabiting extreme environments such as the tundra lakes and streams of North America, and (3) some treatment of the systematics of aquatic insects, which is, after all, a prerequisite for ecological studies. However, these are precluded by the editors on the assumption that such subjects have been adequately reviewed in the recent past. This is probably true. At any rate, the subject matter of the ensuing chapters cuts across the ecological conditions met within all aquatic habitats.

The introduction to this excellent book provides a good historical perspective of a vast subject in four printed pages (at least, as good as one can expect in such a limited space). The following 17 chapters deal with various aspects of the ecology of aquatic insects, but exclude discussion of techniques and procedures for sampling in the aquatic habitat. However, references to recent reviews on various aspects of sampling are supplied. In each chapter it seems obvious that the two major objectives stated in the preface have been satisfied:

(1) contemporary overviews of aquatic insect ecology are presented, and (2) research needs and avenues of investigation that currently seem most promising are highlighted.

Although it is unfair to single out any authors in a book of such uniformly high quality, my own research interests, as well as those of my research group, made me focus on Chapters 2, 3, and 4. Chapter 2 provides a good overview of insect ecological diversity, and the author supports his views by providing specific examples that illustrate these points. It is short and to the point, and like all chapters, offers a superb general as well as specific list of references which assists in bringing the researcher up-to-date with current literature in the field. Chapter 3 is a complete insight into the life histories, life cycles, and phenology of aquatic insects. It follows a logical sequence in how to approach sampling, and points out the shortcomings as well as offers constructive alternatives. The chapter meshes together well and forces one to think about ecological consequences. It also assists the reader by standardizing and elucidating basic patterns and terminology in aquatic entomology. Chapter 4 is more or less a continuation of the previous chapter, providing a comprehensive list of the abiotic factors that influence life cycles and life histories. This chapter is *very* good. It provides the reader with a concise but explicit review of secondary productivity methodologies while providing critical comments on their strengths and weaknesses. Examples used are provided with enough information that one can actually perform the calculations as a personal check. Graphic examples are excellent. Most importantly, the author provides the reader with what he believes are essential points to consider in designing a production experiment, and in general, the direction such studies should be following. The high quality of these three chapters is typical of the book as a whole. The climax of the book is the concluding chapter by H. B. N. Hynes on "Aquatic Insects and Mankind," a chapter that should be read by all entomologists, ecologists, limnologists, and anglers.

In summary, this is an excellent source book for all entomologists and limnologists and, indeed, should be included in the library of all ecologists. Although perhaps too advanced for the beginning student in aquatic entomology, it will prove to be especially valuable for all researchers, whether beginning or already active in this field. The editors should be congratulated for maintaining the uniformity and high quality of all chapters, even though their job was facilitated by, in their own confession, the fact that *all* of the original authors, when approached, accepted with alacrity the invitation to make a contribution.

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(R585)

**Studies in Adaptation. The Behavior of Higher Crustacea.** *Edited by Steve Rebach and David W. Dunham. John Wiley & Sons Inc., New York, NY. 1983. $42.50.*

"This book is at once a valuable reference for the specialist, a stimulating introduction to the fascinating realm of crustacean behavior for the nonspecialist, and an overview of the field for ethologists working with other animal groups." So say editors Steve Rebach and David Dunham in their remarkably immodest preface.

One could hardly quarrel with the first and last parts of their statement. This *is* a comprehensive reference work and it does appear to be an excellent overview for ethologists specializing in other animal groups. However, I feel it falls short of its billing as a stimulating introduction for the nonspecialist.

Since my research interests are with the higher Crustacea and I am not a behaviorist, I qualify as an interested nonspecialist. I found the book to be generally well written, often interesting, and certainly informative, but not what I would call stimulating. Some of the material is too narrow in scope and some is too technical for the nonspecialist (read the chapter on Quantitative and Qualitative Dimensions of Crustacean Aggression, for example).

I was also distracted and occasionally annoyed by the blizzard of abbreviations in some chapters. The extensive selection ranges from dominance hierarchy statistics (DHS) and evolutionary stable strategy (ESS) to my personal favorite, EOOP (for Eggs Only On Pleopods). Also distracting were the occasional editorial lapses. One interesting chapter was so rife with commas as to be nearly unreadable. In another chapter we find

*Orconectes virilis* referred to as *Cambarus virilis*, reversing a generic change that was effected more than 40 years ago.

But this is nitpicking. On balance, Rebach and Dunham have put together an excellent reference work distilled from reviews presented at a symposium organized by the editors of the animal behavior society. In several chapters the authors have done a good job of summarizing complex information in tabular form for quick reference (Michael Salmon's table on decapod courtship interactions is a marvel of synthesis and distillation), and most chapters are detailed in their coverage, carefully written, and interesting.

Information in the book is grouped into five broad categories that take the reader from the general to the specific. Nicely developed evolutionary perspectives lead to modern observations and from there to some interesting speculation on control mechanisms. The serious reader can come out of the book with a genuine appreciation for the evolution, development, control, and study of the behavior of the higher Crustacea. I consider this book a worthwhile acquisition for the personal or institutional library.

D. E. AIKEN

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R505

# BOOKS RECEIVED/LIVRES REÇUS

*June–August 1984*

**Fish, Pathogens and Environment in European Polyculture.** *Edited by J. Olah. Akademiai Kiado, Budapest. 1984. xix + 265 p. ISBN 963-05-3614-5. U.S.$24.* The volume presents the proceedings of an international seminar June 23–27, 1981, devoted to the combined problems of fish health and its interaction with the environment. Interdisciplinary research teams previously organized to tackle specific problems of warmwater fishes, especially carps and silurids, report their findings in 24 papers and concentrate on viral and bacterial diseases, parasites, water quality effects, and immunological prospects. [R586]

**Rearing of Marine Fish Larvae in Japan.** *K. Kuronuma and K. Fukusho. International Development Research Centre, Ottawa, Ont. IDRC-TS47e. 1984. 109 p. ISBN 0-88936-406-0. Cdn$10.00. Available from IDRC, Box 8500, Ottawa, Canada KIG 3H9.* The volume is an outgrowth of a regional workshop held in 1980 in Singapore on "Induced Fish Breeding in Southeast Asia" and makes available details on the Japanese experience on raising marine larval finfish. The authors review the existing information, most of which was previously available only in Japanese, and produce a summary account of the present state of the art in Japan. [R587]

**Diseases of Marine Animals. Vol. II. Introduction, Bivalvia to Scaphopoda.** *Edited by O. Kinne, Biologische Anstalt Helgoland, Hamburg. 1983. vii + p. 467-1038. ISBN 3-9800818-0-X.* One of four volumes, this book critically reviews information on biotic diseases, proliferative disorders, and structural abnormalities of marine Bivalvia, Amphineura, and Scaphopoda. Most of the book is devoted to Bivalvia (96%), with 3% on Amphineura and 1% on Scaphopoda. It is addressed to researchers, teachers, and advanced students in pathology, parasitology, ecology, fisheries biology, and aquaculture. [R588]

**A Manual of Chemical and Biological Methods for Seawater Analysis.** *T. R. Parsons, Y. Maita, and C. M. Lalli. Pergamon Press, Oxford, New York, Toronto. 1984. 173 p. ISBN 0-08-030288-2 (hardcover), ISBN 0-08-030287-4 (flexicover). U.S.$8.95.* The text introduces the practitioner to quantitative analysis of seawater. It builds upon an earlier publication of the Fisheries Research Board of Canada, *A Practical Handbook of Seawater Analysis,* by J. D. H. Strickland and T. R. Parsons, and modifies some of the methods in the former book. It also adds new methods, especially biological techniques, and furnishes a new section on terms and equivalents. [R589]

**Fishes of the World. Second Edition.** *J. S. Nelson. John Wiley & Sons, Inc., New York, NY. 1984. xv + 523 p. ISBN 0-471-86475-7. U.S.$44.95.* A detailed, modern view of fish classification is presented in this updated volume. The book lists the families in evolutionary sequence including common name, range, line drawings of morphological characteristics, description, notes on biology, ecology, and systematics, and recent references. [R590]

**Population Biology. The Coevolution of Population Dynamics and Behavior.** *J. M. Emlen. MacMillan Publishing Company, New York, NY. 1984. xii + 547 p. ISBN 0-02-333660-9.* Population dynamics, dispersal, sociobiology, the genetic basis of adaption, and life history theory are covered in the book, which can serve as a text for advanced students, a synthesis and compendium of new ideas and directions for future research, and source of key references to literature through 1982. [R591]

**Comparative Analyses of Fish Populations in Naturally Acidic and Circumneutral Lakes in Northern Wisconsin.** *J. G. Wiener. U.S. Fish and Wildlife Service, Eastern Energy and Land Use Team. 1983. 107 p. FWS/OBS-80/40.16. Available in limited numbers from Eastern Energy and Land Use Team, U.S. Fish and Wildlife Service, Rt. 3, Box 44, Kearneysville, WV 25430, USA.* Parameters compared include community structure, growth and condition, serum calcium concentrations, trace metal accumulation, and bilateral asymmetry of anatomical characteristics. [R592]

**Rocky Mountain Acidification Study.** *J. H. Gibson, J. N. Galloway, C. Schofield, W. McFee, R. Johnson, S. McCarley, N. Dise, and D. Herzog. U.S. Fish and Wildlife Service, Eastern Energy and Land Use Team. 1983. 137 p. FWS/OBS-80/40.17. Available in limited numbers from Eastern Energy and Land Use Team, U.S. Fish and Wildlife Service, Rt. 3, Box 44, Kearneysville, WV 25430, USA.* This report evaluates sensitivity and potential effects of acidic deposition in watersheds characteristic of the Rocky Mountain region. It evaluates the extent of current acidification and potential increasing acidification in the future, evaluates the results in terms of fish populations, and develops recommendations for assessing future trends in water chemistry and fishery resources. [R593]

**Zooplankton of the Great Lakes. A Guide to the Identification and Ecology of the Common Crustacean Species.** *M. D. Balcer, N. L. Korda, and S. I. Dodson. The University of Wisconsin Press, Madison, WI. 1984. xi + 174 p. ISBN 0-299-09820-6. U.S.$35.* This laboratory manual will be welcomed by zoologists, limnologists,

hydrobiologists, fish ecologists, and those who study or montor water quality. It includes taxonomic keys, a checklist of species, notes on distribution and abundance, and, for the 34 most common species, line drawings and sections on their taxonomy and biology. [R594]

**The Ecology of Freshwater Phytoplankton.** *C. S. Reynolds. Cambridge University Press, New York, NY. 1984. xii + 384 p. ISBN 237823. U.S.$54.50 hardcover, U.S.$24.95 paperback.* The book deals with lifestyles of phytoplankton from the point of view of the organisms' needs and adaptive responses to them, including mechanics of suspension, spatial and temporal distribution, photosynthetic activity, nutrients, growth and survival, loss processes, and periodicity in phytoplankton populations. [R595]

**Toxic Contaminants in the Great Lakes.** *Edited by J. O. Nriagu and M. S. Simmons. John Wiley & Sons, New York, NY. 1984. xiii + 527 p. ISBN 0471-89087-1. U.S.$95.* Contributors to this volume provide a perspective on toxic substances in the Great Lakes, their entry into, movement through, persistence in, and effects on the Great Lakes and their biota. The book takes a step towards providing regulatory agencies the information they need to create more effective controls. Comprehensive reviews concentrate on chlorinated hydrocarbons, polynuclear aromatic hydrocarbons, toxaphene, and mirex, as well as metals such as mercury, lead, cadmium, and selenium. [R596]

**Algal Biology: A Physiological Approach.** *W. M. Darley. Blackwell Scientific Publications, Inc., Oxford. 1982. viii + 168 p. ISBN 0632-00608-0. U.S.$15.60 paperback.* This introductory text on biology of algae is organized by habitat, with emphasis on experimental rather than descriptive science, and integrates field and laboratory results to explain algae's success in nature. [R597]

**Reproduction in Reef Fishes.** *R. E. Thresher. T. F. H. Publications, Inc., Neptune, NJ. 1984. 399 p. ISBN 0-87666-808-2. U.S.$39.95.* Breeding habits of over 70 families of reef fishes found in marine aquaria are detailed in richly illustrated fashion. Over 300 photographs are in color. The book is aimed at both the professional biologist and marine aquarist who wishes to spawn and rear reef fishes in small aquaria. [R598]

**Annotated Species List of Marine Planktonic Copepods Occurring on the Shelf and Upper Slope of the Northwest Atlantic (Gulf of Maine to Ungava Bay).** *M. J. Tremblay and J. T. Anderson. 1984. Can. Spec. Publ. Fish. Aquat. Sci. 69: 12 p. ISBN 0-660-11585-9. $3 in Canada, $3.60 other countries.* Occurrence of planktonic copepods in shelf and slope waters to 1000 m depth was reviewed and an annotated species list derived, based on taxonomic and distributional information published since 1969. [R599]

**Biological Oceanographic Processes. Third edition.** *T. R. Parsons, M. Takahashi, and B. Hargrave. Pergamon Press, Oxford, New York. 1984. xiii + 330 p. ISBN 0-08-030766-3 (hardcover), ISBN 0-08-030765-5 (flexicover). U.S.$40 hardcover, U.S.$19.75 flexicover.* This revised textbook is aimed at students, physical oceanographers, engineers, hydrologists, and fisheries scientists. It leads the reader through subjects ranging from distribution of marine organisms, to discussions on trophic relations, to a final chapter on practical applications of biological oceanography to fisheries and pollution problems. [R600]

# ANNOUNCEMENTS/AVIS

## Second Annual Meeting of the Aquaculture Association of Canada and 9th Atlantic Regional Fish Health Workshop

### First Announcement and Call for Papers

The Second Annual Meeting of the Aquaculture Association of Canada and the 9th Atlantic Regional Fish Health Workshop will be held together in Halifax, Nova Scotia, from March 5 to 9, 1985, at the Hotel Nova Scotian. The Aquaculture Association of Nova Scotia will cosponsor the meeting.

The program will include invited speakers and submitted papers (oral and poster). Three special symposia are planned: Aquaculture and Fish Health Protection Regulations, Aquaculture and the Law, and Furunculosis in Salmonids. Aquaculture topics will include engineering and technological development, financial and economic considerations, nutrition, disease, genetics, education and training, and seedstock supply. The Fish Health Workshop sessions will include bacterial and viral diseases, parasites, nutrition, and physiology.

For further information contact the Program Coordinator, Gary Newkirk, Biology Department, Dalhousie University, Halifax, N.S. B3H 4J1.

## Deuxième réunion annuelle de l'Association aquicole du Canada et 9e atelier de la Région de l'Atlantique sur la santé des poissons

### Premier avis et demande d'articles

La deuxième réunion annuelle de l'Association aquicole du Canada et le 9e atelier de la Région de l'Atlantique sur la santé des poissons auront lieu simultanément à Halifax (Nouvelle-Écosse), de 5 au 9 mars 1985, à l'hôtel Nova Scotian. La réunion sera coparrainée par l'Association aquicole de la Nouvelle-Écosse.

Le programme prévoit la participation de conférenciers invités et la présentation d'articles (exposés oraux et séances d'affichage). Trois séances spéciales devraient avoir lieu : l'aquiculture et les règlements sur la protection de la santé du poisson, l'aquiculture et la loi et la furonculose chez les salmonidés. Voici quelques-uns des sujets qui seront abordés : développement technique et technologique, questions financières et économiques, nutrition, maladies, génétique, éducation et formation et approvisionnement en stocks reproducteurs. Au cours de l'atelier sur la santé du poisson, il sera question de maladies bactériennes et virales, de parasites, de nutrition et de physiologie.

Pour plus d'information, communiquez avec le coordonnateur du programme, Gary Newkirk, au département de biologie de l'Université Dalhousie, Halifax (N.-É.) B3H 4J1.

## International Large River Symposium (LARS)

An International Large River Symposium (LARS) is planned for September 1986 near Toronto, Ontario, Canada.

The major aim of this symposium is to provide an understanding of the management of large rivers for fish production. This will be accomplished by synthesizing and distilling, in a mission-oriented approach, the best science and philosophy on fish production into papers directly applicable to the management of fisheries resources in large rivers.

The symposium will consist of a series of overview papers describing the production processes of rivers, dealing preferentially with large rivers, case history papers describing large rivers throughout the world, and synthesis papers dealing with global values of production yield and standing stocks, and considering effective management strategies on large rivers.

The proceedings of the symposium will be published. Anyone wishing to be placed on the mailing list or to contribute to the symposium should write to the chairman of the Steering Committee at the following address, stating their areas of interest and expertise:

Douglas P. Dodge, Ph.D.
Chairman, Steering Committee
International Large River Symposium
c/o Fisheries Branch
Ontario Ministry of Natural Resources
99 Wellesley Street West
Toronto, Ont. M7A 1W3

## Colloque international sur les grands cours d'eau

Un colloque international sur les grands cours d'eau devrait avoir lieu en septembre 1986, près de Toronto (Ontario), Canada.

L'objectif principal du colloque est d'améliorer les connaissances sur la gestion des grands cours d'eau, aux fins de la production de poisson. Pour ce faire, on synthétisera et l'on résumera les meilleurs ouvrages scientifiques et philosophiques traitant de production de poisson de façon à obtenir des documents pouvant servir directement à la gestion des ressources halieutiques dans les grands cours d'eau.

Le colloque permettra l'examen d'une série d'articles généraux décrivant les méthodes de production utilisées dans certains cours d'eau et, de préférence, dans de grands cours d'eau, d'articles précis décrivant certains grands cours d'eau du monde entier et d'articles de synthèse traitant des valeurs globales du rendement de la production et des stocks permanents, et examinant des stratégies de gestion efficaces pour les grands cours d'eau.

Le compte rendu du colloque sera publié. Toute personne désirant avoir son nom sur la liste d'envoi ou désirant contribuer au colloque devrait écrire au président du comité directeur, à

l'adresse suivante, en précisant ses domaines d'intérêt et de spécialisation :

Douglas P. Dodge, Ph.D.
Président, comité directeur
Colloque international sur les grands cours d'eau
a/s Direction des pêches
Ministère des Richesses naturelles de l'Ontario
99 Wellesley Street West
Toronto (Ont.) M7A 1W3

## First and Only Call for Papers:

**Common strategies of anadromous and catadromous fishes: an international symposium, March 9–13, 1986, Boston Park Plaza, Boston, Massachusetts, USA (Sponsored by Northeastern Division, American Fisheries Society)**

Anadromous and catadromous fishes encounter a suite of similar problems during the course of their life histories, no matter how diverse their phylogeny. This international conference will explore, compare, and contrast the survival strategies of diadromous fishes. Researchers, students, and managers of diverse fish groups from around the world will exchange ideas, approaches, and findings to gain broader perspectives, greater awareness, and new directions for diadromous research and management.

The conference will be held March 9–13, 1986, in the Boston Park Plaza, Boston, Massachusetts, and will consist of four one-day sessions focused on the following topics:

Session 1: Utilization of the Freshwater Habitat

Convener: C. M. Moffitt
Idaho Cooperative Fishery Research Unit
University of Idaho, Moscow, ID 83843
(208) 885-7047

Session 2: Transition to and from the Marine Environment

Convener: R. L. Saunders
Department of Fisheries and Oceans
Biological Station, St. Andrews, N.B. E0G 2X0
(506) 529-8854

Session 3: Ocean Migrations

Convener: M. J. Dadswell
Department of Fisheries and Oceans
Biological Station, St. Andrews, N.B. E0G 2X0
(506) 529-8854

Session 4: Recruitment Mechanisms

Convener: R. J. Klauda
Applied Physics Laboratory
Johns Hopkins University, Shadyside, MD 20764
(301) 867-7000

The program will consist of oral presentations of invited and contributed papers and a poster session. Information gathered for over 15 diadromous species will be presented by invited speakers representing eight countries, five Canadian provinces, and 10 U.S. states. Persons wishing to contribute a paper or poster are urged to contact the convener of the most appropriate session. English abstracts of 300 to 500 words must be submitted by December 31, 1984.

For additional information, contact M. J. Dadswell, Symposium Chairman.

## Première et unique invitation à présenter des communications :

**Strategies courantes des poissons anadromes et catadromes : un symposium international qui se tiendra du 9 au 13 mars 1986 au Boston Park Plaza à Boston, Massachusetts (É.-U.) (parrainé par la Northeastern Division de l'American Fisheries Society).**

Les poissons anadromes et catadromes doivent résoudre une série de problèmes semblables au cours de leur vie et ce, quelle que soit leur phylogénie. Au cours de cette conférence internationale, on examinera, comparera et différenciera les stratégies de survie des poissons diadromes. Des chercheurs, des étudiants et des gestionnaires de divers groupes de poisson du monde entier échangeront leurs idées, leurs approches et leurs découvertes afin d'élargir leurs perspectives, d'affiner leur perception et de connaître de nouvelles orientations dans les domaines de la recherche et de la gestion des poissons diadromes.

La conférence aura lieu du 9 au 13 mars 1986 au Boston Park Plaza à Boston, Massachusetts. Elle comprendra quatre séances d'une journée portant sur les sujets suivants :

Séance 1 : Utilisation de l'habitat dulçaquicole
Animateur : C. F. Moffitt
Idaho Cooperative Fishery Research Unit
University of Idaho, Moscow, ID 83843
(208) 885-7047

Séance 2 : Le poisson et le milieu marin : entrée et sortie
Animateur : R. L. Saunders
Pêches et Océans, Station de biologie
St. Andrews (N.-B.) E0G 2X0
(506) 529-8854

Séance 3 : Migrations océaniques
Animateur : M. J. Dadswell
Pêches et Océans, Station de biologie
St. Andrews (N.-B.) E0G 2X0
(506) 529-8854

Séance 4 : Mécanismes de recrutement
Animateur : R. J. Klauda
Applied Physics Laboratory
Johns Hopkins University, Shadyside, MD 20764
(301) 867-7000

Il y aura des lectures de communications, des exposés faits par les conférenciers invités et des séances d'affiches. Des informations touchant 15 espèces de poissons diadroms seront communiquées par les conférenciers invités qui représentent huit pays, cinq provinces canadiennes et 10 États américains. Les personnes désirant présenter une communication ou une affiche sont priées d'entrer le plus tôt possible en relation avec l'animateur de la séance la plus appropriée. Les résumés, en anglais, de 300 à 500 mots doivent être présentés au plus tard le 31 décembre 1984.

Pour plus de renseignements, veuillez prendre contact avec M. J. Dadswell, qui est le président du symposium.

# COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

## Articles


The quantification of stream drift **J. D. Allan and E. Russek**

Wound healing in the bottlenose dolphin (*Tursiops truncatus*) **L. J. Bruce-Allan and J. R. Geraci**

Movements of tagged American lobsters, *Homarus americanus*, off southwestern Nova Scotia **A. Campbell and A. B. Stasko**

Modelling winter oxygen depletion rates in ice-covered temperate zone lakes in Canada **J. Babin and E. E. Prepas**

Hotelling's $T^2$ to identify the origin of Atlantic salmon (*Salmo salar*) in a mixed-stock fishery **D. G. Reddin and R. K. Misra**

Work satisfaction and community attachment among fishermen in southwest Nova Scotia **R. Apostle, L. Kasdan, and A. Hanson**

Gas supersaturation as a cause of early spring mortality of stocked trout **J. A. Mathias and J. Barica**

Experimental and field evidence for inter- and intraspecific competition in two freshwater fishes **J. M. Hanson and W. C. Leggett**

Initial egg weight, time to maximum alevin wet weight, and optimal ponding times for chinook salmon (*Oncorhynchus tshawytscha*) **P. J. Rombough**

Survival of eggs and alevins of Atlantic salmon (*Salmo salar*) in relation to the chemistry of interstitial water in redds in some acidic streams of Atlantic Canada **G. L. Lacroix**

Cellular phosphorus concentration as a criterion for trophic status in rapidly flushed lakes **P. D. Uttormark and M. L. Hutchins**

The effect of production variability on financial risks of freshwater prawn farming in Hawaii **K. C. Samples and P. S. Leung**

Variation in length and body depth of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in southern British Columbia **T. D. Beacham and C. B. Murray**

Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes **K. D. Hyatt and J. G. Stockner**

Dispersion and retention of anadromous rainbow smelt (*Osmerus mordax*) larvae in the middle estuary of the St. Lawrence River **P. Ouellet and J. J. Dodson**

Morphology and systematics of the nemertean *Pseudocarcinonemertes homari* (Hoplonemertea:Monostilifera) from the American lobster, *Homarus americanus* **L. S. Uhazy, D. E. Aiken, and A. Campbell**

Aspects of the biology of *Pseudocarcinonemertes homari* and its association with the American lobster, *Homarus americanus* **D. E. Aiken, S. L. Waddy, and L. S. Uhazy**

Immunofluorescent localization of American lobster egg yolk protein in the alimentary tract of the nemertean *Pseudocarcinonemertes homari* **S. L. Waddy and D. E. Aiken**

Geographic distribution and seasonal occurrence of the nemertean *Pseudocarcinonemertes homari* on the American lobster, *Homarus americanus* **J. Brattey, A. Campbell, A. E. Bagnall, and L. S. Uhazy**


## Notes


Juvenile lobster (*Homarus americanus*) do not require dietary ascorbic acid **J. C. Kean, J. D. Castell, and D. J. Trider**

Synthesis of dehydroascorbic acid by subadult lobsters (*Homarus americanus*) **L. M. Desjardins, J. D. Castell, and J. C. Kean**

Radiotracer estimation of microbial biomass in lake sediment **G. G. Marten**

Strontium labelling for verifying daily growth increments in the statolith of the short-finned squid (*Illex illecebrosus*) **G. V. Hurley, P. H. Odense, R. K. O'Dor, and E. G. Dawe**

Influence of light on the alkaline phosphatase activity of *Selenastrum capricornutum* (Chlorophyceae) in streams **R. L. Klotz**

**Perspectives**

The human factor in fishery resource management — **J. D. Pringle**

**Letters and comments/Lettres et commentaires**

Comment on fecundity of chinook salmon and its relevance to life history theory — **D. G. Hankin and R. McKelvey**

Reply — **M. C. Healey and W. R. Heard**

**Book reviews/Comptes rendus**

Marine and coastal systems of the Quoddy region, New Brunswick (edited by Martin L. H. Thomas) — **M. Risk**

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Books received/Livres reçus
Corrections to recent publications/Corrections sur récents publications
Announcements/Avis

# Guide for Authors

## Introduction

We welcome manuscripts reporting significant new information in fisheries and aquatic sciences. Manuscripts may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and cover numerous disciplines including biology and ecology of marine and freshwater organisms, physiology, toxicology, genetics, limnology, oceanography, economics, disease, and management.

Manuscripts are selected for publication according to the extent and significance of new knowledge or ideas presented. Preference will be given to those whose experimental results emphasize causal mechanisms underlying observed phenomena rather than pure description and fact. Manuscripts should lead to identifiable conclusions or synthesis, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. Their novelty must relate to more than the particular (a certain year, place, taxon, chemical compound) and their contribution to science must clearly be beyond the confirmatory state.

Manuscripts submitted should be as comprehensive as possible; research fragments are generally unacceptable. If a single paper cannot be produced, then closely related papers should be cross-referenced and submitted together. The paper should not be submitted or accepted for publication elsewhere.

The *Journal* considers the following types of contributions:

**Articles:** Studies of broad scope that are original contributions to science.

**Notes:** Reports of significant new knowledge arising from problems with narrow limits or important findings that warrant immediate publication before broader studies are complete. Notes should occupy no more than 3 printed (9 manuscript) pages.

**Reviews:** Detailed critical appraisals of broad areas of investigation, particularly those that have developed rapidly in recent years.

**Perspectives:** Essays of opinion or hypothesis on aquatic science of concern to the professional and layman. References are desirable; informal style is welcome.

**Comments:** Opinion on topics recently discussed in the *Journal*; preferred maximum length, 500 words.

## Manuscript Submission

Submit manuscripts in triplicate to the Editor, accompanied by a covering letter that (1) states the main points and significance of the work, (2) accepts the mandatory $44 page charge, (3) suggests potential referees, and (4) identifies other manuscripts containing the same or similar information. The page charge can be waived only if the work is of unusually high quality and grant support is lacking. Original typescripts and figures (except halftones) are best retained by the author until requested.

Each manuscript is normally submitted to two referees for appraisal before final evaluation by an editor. However, the Editor will return unreviewed those manuscripts that do not fall within the *Journal's* editorial policy or scope.

## Editorial Practices

The *Council of Biology Editors Style Manual* (5th ed. CBE, 9650 Rockville Pike, Bethesda, MD 20814) is used as the authority in matters of form. The standards for spelling are either *Webster's Third International Dictionary* or the *Oxford English Dictionary* and *le Grand Larousse encyclopédique*. Authors are responsible for consistency in spelling. Titles of periodicals are abbreviated as in *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103). Authors are responsible for ensuring the accuracy and completeness of their reference list. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (4th ed. 1980), Spec. Publ. No. 12, American Fisheries Society. All measurements must be metric, use SI symbols in most instances (exceptions noted in editorial in *Journal*, Vol. 40, No. 12), and adhere to the *Canadian Metric Practice Guide* CAN3-Z234.1-79 (Canadian Standards Association, 178 Rexdale Boulevard, Rexdale, Ont. M9W 1R3).

Series titles should be avoided. An abstract is required for all manuscripts and should state concisely, in up to 175 words, what was done, found, and concluded.

Proofs are sent to the author, who is responsible for correcting errors in typesetting. *Alterations to the content must be avoided.*

Fifty reprints are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent with the proofs).

## Preparation of Manuscripts

### General Guidelines

Movement of manuscripts through review channels and the editorial office is greatly expedited if manuscripts are prepared in *Journal* style and format. When in doubt about specific details, consult a current issue of the *Journal*. General guidelines follow.

Type the manuscript on white paper, preferably 21.5 × 28 cm (8.5 × 11 in.), on only one side of the page. If possible, use paper with lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Type only the title, authors' names and affiliations, and related footnotes on the first page. Number all pages beginning with the title page, including those for tables and captions for illustrations.

Double-space all parts of the manuscript, including tables, captions for tables and figures, footnotes, and the reference list. Underline only material that is to be printed in italics.

Do not use all capitals anywhere in the manuscript.

Use the name-and-year system for literature citations.

### Checklist for Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables and figures and the text, or within the text? Should some of the data be made available separately in a data or manuscript report or at a data repository?

If statistical analysis is included, is it subordinate to the research? When probability statements are made, are only the statistical tests cited and unnecessary statistical tables excluded?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report? Does the *abstract* give the essentials of the new knowledge? Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem? Are details of *materials and methods* limited to what scientists need to understand the design of the study and to judge the adequacy of the data? Are generalizations from the *results* supported by the data provided? Are findings distinguished from inferences? Is the *discussion* limited to interpretation and significance of the findings?

The most common technical problems in submitted manuscripts are listed below. Authors can hasten the processing of their papers if they pay attention to these points during manuscript preparation.

1) Insert bibliographic strip before the abstract (Authors, date, title, Can. J. Fish. Aquat. Sci.).

2) Limit abstract to one paragraph of about 175 words.

3) Double-space all elements of the manuscript, including references, table captions, and figure legends.

4) Avoid exclusive use of capitals eveywhere in the manuscript, including headings, table captions, and figure legends.

5) Underline only Latin names of organisms and certain statistical and mathematical notation to indicate italics.

6) Use correct SI symbols for units of measure in figures, tables, and text. Place a zero before the decimal for numbers less than unity.

7) Avoid ambiguous forms such as g $C/m^2/d$; use g $C \cdot m^{-2} \cdot d^{-1}$.

8) Identify test used to test statistical significance and give probability value. No reference is needed for common statistical tests.

9) In the text, generalize from tables and figures; avoid repeating all the details. Be sure each table and figure can stand on its own and is referred to in the text in numerical order. The captions should explain the purpose of the table or figure.

10) Include acknowledgments section at manuscript stage, not when galley proofs arrive.

11) Provide the person's initials and mailing address when referring to personal communications.

12) Delete unnecessary references that do not apply directly to the problem.

13) Check references carefully against text citations and vice versa to ensure exact correspondence. Provide an availability statement for less easily retrieved material, e.g. available from Department of Economics, Simon Fraser University, Burnaby, B.C. V5A 1S6.

14) Delete commas between name and date in citations such as (Smith 1900) and do not underline "et al."

15) Replace 10″ in table headings and figure axes with appropriate SI prefixes or use words (e.g. thousands).

16) Photocopies of figures, except halftones, are appropriate for review purposes. Send photographic prints of figures, or originals if they do not exceed 21.5 × 28 cm, on request for publication. Use the same type of lettering throughout if possible.

## Parts of the Manuscript

### Organization

Organize the manuscript on the basis of the purpose or scope of the study as stated in the introduction. Ensure that the title and headings are in harmony with the statement of purpose.

Before writing any of the manuscript, list tentative headings in as few ranks as possible. Rework them until they appear to allow logical development for the reader; usually, chronological order is not effective. The findings will be more readily appreciated if methods, findings, and discussion are given in separate sections.

Organize tables and figures to facilitate comparisons, grouping related data in as few tables and figures as feasible. As far as possible, make the tables and figures clear without reference to the text.

Begin sections and paragraphs with topic sentences containing generalizations that lead readily to the particulars. Giving a conclusion first and then supporting it not only improves readability but also facilitates assessment by other scientists. Failure to give the most newsworthy generalizations first is one of the most prominent shortcomings in presentation of manuscripts.

See that everything in each section is relevant to the heading, and everything in each paragraph to the topic (opening) sentence.

Before writing any paragraphs, try writing the topic sentences for all of them and arranging these in appropriate order.

### Title

Limit the title to what is documented in the manuscript. It is the key to the article and should clearly and concisely reveal what appears in the paper itself. The title serves two functions: (1) it allows the reader to judge whether or not the article is of potential interest and (2) it should provide enough information to permit the reader to judge the scope and potential importance of the article. Words in the title should convey a maximum amount of information and identify the nature of the research, organism used, and where appropriate, the technical approach (e.g. X ray, chromatography, mathematical analysis). Titles should not begin with a numeral or introductory prepositions such as "On" or "Towards" or expressions such as "A contribution to ..." or "Investigations on ..." Good titles greatly assist scientists and librarians in using scientific literature and aid indexers preparing titles for keyword indexes.

### Abstract

The abstract should succinctly mirror the content and emphasis of the paper in about 175 words. Like the title, the abstract enables readers to determine the paper's content and decide whether or not they need to read the entire article. Begin

the abstract with the main conclusion from the study, and support it with the relevant findings. Limit details of methods to those needed in understanding what was done, and work them into statements of findings. Avoid using phrases such as "... is discussed" or "... was found"; be specific. As the abstract is often divorced from the main body of the paper by abstracting and indexing services and is the only part of a paper some readers ever see, it is important that it accurately reflect the paper's contents.

### Introduction

Limit the introduction largely to the scope, purpose, and rationale of the study. Restrict the literature review and other background information to that needed in defining the problem or setting the work in perspective. Try beginning with the purpose or scope of the work, defining the problem next, and adding guideposts to orient the reader. An introduction generally need not exceed 375–500 words.

### Materials and Methods

Materials and Methods provides the framework for getting answers to the questions concerned in the purpose of the work.

Limit the information on materials and methods to what is needed in judging whether the findings are valid. To facilitate assessment, give all the information in one section when possible. Refer to the literature concerning descriptions of equipment or techniques already published, detailing only adaptations. Often, it helps to begin statements on procedures with a phrase indicating the purpose, such as "To determine ... we ..." If the section is long, consider using subheadings corresponding to headings for the findings.

### Results

Limit the results to answers to the questions posed in the purpose of the work, and digest them as comprehensively as possible. Give the findings as nearly as possible in the terms in which the observations or measurements were made and so avoid confusion between facts and inferences. State noteworthy findings to be noted in each table and figure, and avoid restating in the text what is clear from the titles. Material supplementary to the text can be archived in the report literature or a recognized data depository and referenced in the text.

### Discussion

Limit the discussion to giving the main contributions of the study and interpreting particular findings, comparing them with those of other workers. Emphasis should be maintained on synthesis and interpretation and exposition of broadly applicable generalizations and principles. If these are exceptions or unsettled points, note them and show how the findings agree or contrast with previously published work. Limit speculation to what can be supported with reasonable evidence. End the discussion with a short summary of the significance of the work and conclusions drawn. If the discussion is brief and straightforward, it can be combined with the results section.

### Acknowledgments

We strongly urge authors to limit acknowledgments to those who contributed substantially to scientific and technical aspects of the paper, gave financial support, or improved the quality of the presentation. Avoid acknowledging those whose contribution was clerical only.

### References

References should be selected judiciously and be largely restricted to significant, published literature. References to unpublished data, manuscripts in preparation or submitted to other journals, progress reports, and unpublished papers given at annual meetings may not be cited in the reference list but may be noted in the text as unpublished data or personal communications (include mailing addresses). If consultants' reports or other documents of limited circulation must be cited, they should carry with them an availability statement explaining where the document can be obtained. Citations of literature in the text should be carefully checked against those in the reference list and vice versa to ensure exact correspondence. Nearly every manuscript submitted to the *Journal* contains errors in the references.

### Tables

Tables are used to present repetitive data and should be as economical of space as possible.

Design tables to fit within either a column or page of the *Journal*.

Type each on a separate page and number with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Table captions should be succinct and identify the purpose of the table sufficiently well to allow the table to stand on its own.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines.

### Figures

Provide photographic reproductions or the original artwork (no larger than 21.5 × 28 cm) of each illustration. If submitting photographs, type the author's name and figure name on a strip of paper and fasten to the back of the print. Do not write on the illustration itself. Provide two photocopies of line illustrations and two sets of any photographs for review purposes.

Design figures to fit a 1-, 1½-, or 2-column width of the *Journal* and ensure that all lettering, numerals, and symbols are legible, neat, and at least 1.5 mm high when reduced. Figures should not be mounted, stapled, or clipped. When possible, figures should be grouped and be done with the same or similar type of lettering.

Type legends in succession on a separate page. Add bar scales to maps, photomicrographs, equipment diagrams, etc.

Where each figure is first referred to, type "Fig. — near here."

Computer-generated figures should be avoided if possible, as they usually reproduce poorly. Dot-matrix printers cannot produce sufficiently dark, solid lines to ensure legibility. Figures drafted in black india ink are always preferable. If sheets of printed characters are used, be sure they adhere completely.

Draft rather than type axis labels for graphs.

Color plates are very expensive to produce and should only be used where the color being presented is essential to the understanding of the text. Extra costs for the reproduction of color plates are usually charged to the author. Submit only the most outstanding photographs for color reproduction. We prefer to use color photographs, but will accept drawings, color negatives, slides, or film positives.

### Mathematical Expressions, Equations, and Formulae

Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulae. In the various expressions, place each component in its correct position.

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the number *one*, and between the capital *O* and the numeral *zero*. Make other explanatory notes similarly.

## Appendix

### Abbreviations

Abbreviate terms denoting units of weight and measurement in the text only when they are preceded by numerals.

| | |
|---|---|
| Becquerel | Bq |
| calorie | cal |
| centimetre | cm |
| centimetre, square | $cm^2$ |
| centimetre, cubic | $cm^3$ |
| centimetre per gram per second | $cm \cdot g^{-1} \cdot s^{-1}$ |
| coulomb | C |
| day | d |
| decimetre | dm |
| degree Celsius | °C |
| degrees of freedom | df |
| gram | g |
| hectare | ha |
| hertz | Hz |
| hour | h |
| joule | J |
| kilometre | km |
| litre | L |
| lumen | lm |
| lux | lx |
| metre | m |
| metre, square | $m^2$ |
| metre, cubic | $m^3$ |
| micrometre | µm |
| milligram | mg |
| millilitre | mL |
| millimetre | mm |
| millimetre, square | $mm^2$ |
| minute | min |
| molar mass | *M* |
| mole | mol |
| month | mo |
| Pascal | Pa |
| second | s |
| standard deviation | SD |
| standard error | SE |
| tonne | t |
| volt | V |
| volume | vol |
| watt | W |
| week | wk |
| year | yr |

### Dates

Dates may be written in the sequence day–month–year without internal punctuation (On 9 October 1983 the ...), or the alternative sequence month–day–year may be employed with the year set off by commas before and after it (On October 9, 1983, the ...).

### Reference Citations in Text

*Name-and-year system*

The *Journal* uses the name-and-year system of citation; that is, the surname of the author(s) and the year of publication are inserted in the text at an appropriate point: "Brown (1983) compared ..." or "... were compared (Brown 1983)." If the reference has more than two authors, include only the surname of the first author followed by "et al." (not italicized): "Brown et al. (1983) compared ..." or "... were compared (Brown et al. 1983)."

*Personal communications*

Personal communications are not listed in the reference list. Using parentheses in the text, state the name and mailing address of the communicator followed by "pers. comm."

*Unpublished data*

If the unpublished book or article has been accepted for publication, list it in the reference list section followed by the notation "(In press)." Only those manuscripts that are in galley or page proof or for which there is an acceptance letter can be considered in press. If the article is submitted but not yet accepted, state the name and address of the author of the unpublished material followed by the notation "unpubl. data" in the text and do not include it in the reference list.

### Reference Lists

The following bibliographic citations illustrate the punctuation, style, and abbreviations (according to *Serial Sources for the BIOSIS Data Base*) for references.

*Journal article*

PETERMAN, R. M. 1982. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. 39: 1444–1452.

*Entire issue of journal*

GORDON, D. C. JR., AND A. S. HOURSTON [ED.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40 (Suppl. 1): 1–365.

*Book in a series*

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

*Book not in a series*

LEBLOND, P. H., AND L. A. MYSAK. 1978. Waves in the ocean. Elsevier, New York, NY. 602 p.

*Part of book*

HEALEY, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia, p. 203–229. *In* W. J. Neil and D. C. Himsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, OR.

*Corporate author*

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1975. Standard methods for the examination of water and wastewater. 14th ed. Washington, DC. 1193 p.

*Theses*

KUTTY, M. N. 1966. Some studies on the respiratory quotient in goldfish and rainbow trout. Ph.D. thesis, Univ. Toronto, Toronto, Ont. 102 p. Natl. Libr. Can., Can. Theses Microfilm No. 646.

*Reports*

SMITH, J. E. 1981. Catch and effort statistics of the Canadian groundfish fishery on the Pacific coast in 1980. Can. Tech. Rep. Fish. Aquat. Sci. 1032: 90 p.

*Translation*

KOIKE, A., AND M. OGURA. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64: 1–11. (Transl. from Japanese by Can. Transl. Fish. Aquat. Sci. 4950, 1983)

## Time

A colon should be used as the separator between hour and minute and between minute and second. The symbols "h," "min," and "s" are not used, since they are the symbols for hour, minute, and second in the sense of duration or the length of time. Thus "12 h 30 min" expresses a measured time of twelve hours and thirty minutes duration whereas 12:30 refers to the time of day.

## Word List

The spelling of the following words is frequently inconsistent in submitted manuscripts. We prefer that authors adhere to the *Journal's* house style for these commonly used terms:

age-class (n.)
age-group (n.)
aquaculture (n.)
Arctic char (n.)
brackish water (n.)
brackish-water (adj.)
chi-square (n., adj.)
cold water (n.)
cold-water (adj.)
deep sea (n.)
deep-sea (adj.)
deep water (n.)
deepwater (adj.)
freshwater (n., adj.)
fresh water (n.)
groundwater (n., adj.)
hard water (n.)
hardwater (adj.)
headwater (n., adj.)
lake water (n., adj.)
meltwater (n., adj.)
open water (n.)
open-water (adj.)
percent (n.)
salt water (n.)
saltwater (adj.)
sea-run (adj.)
seawater (n., adj.)
shallow water (n.)
shallow-water (adj.)
short term (n.)
short-term (adj.)
size-class (n.)
snowmelt (n.)
soft water (n.)
softwater (adj.)
tidewater (n., adj.)
*t*-test (n., adj.)
warm water (n.)
warmwater (adj.)
year-class (n.)
young-of-the-year (n., adj.)

# Guide des auteurs

## Introduction

Les manuscrits comportant une information nouvelle dans le domaine des sciences halieutiques et aquatiques sont les bienvenus. Ils peuvent se rapporter aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influencent les systèmes de production aquatiques, et couvrir de nombreuses disciplines, y compris biologie et écologie des organismes marins et dulçaquicoles, physiologie, toxicologie, génétique, limnologie, océanographie, économique, maladies et gestion.

Les critères de sélection des manuscrits dépendent de l'étendue et de l'importance des connaissances ou idées nouvelles qu'ils contiennent. On donnera la préférence à ceux dont les résultats expérimentaux font ressortir les mécanismes sous-jacents aux phénomènes observés plutôt qu'une simple description ou énoncé de fait. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles en faisant plus que corroborer des faits.

Les manuscrits soumis devraient être aussi complets que possible ; des fragments de recherche sont généralement inacceptables. S'il est impossible de produire un seul article, on devra soumettre ensemble des articles étroitement liés entre eux, avec références croisées. L'article ne doit pas avoir été soumis ou accepté pour publication ailleurs.

Le *Journal* considère les types de contributions suivants :

**Articles :** études d'une portée générale, constituant des contributions inédites à la science.

**Notes :** communications brèves signalant une connaissance nouvelle et significative découlant de problèmes étroitement limités et facilement définis, ou d'importantes découvertes qui méritent d'être publiées avant que des études plus vastes soient terminées. Les notes ne doivent pas dépasser 3 pages imprimées (9 pages de manuscrit).

**Critiques :** appréciations critiques détaillées de vastes champs de recherche, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

**Perspectives :** essais portant sur une opinion ou une hypothèse relative aux sciences aquatiques qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

**Commentaires :** opinions sur des sujets récemment exposés dans le *Journal*, et, de préférence, ne dépassant pas 500 mots.

## Soumission des manuscrits

Les manuscrits doivent être soumis au rédacteur en triplicata, et accompagnés d'une lettre mentionnant : (1) les principaux points et l'importance du travail, (2) l'acceptation des frais de publication obligatoires de 44 $ par page, (3) des suggestions quant aux arbitres éventuels et (4) une mention d'autres manuscrits contenant une information identique ou qui se rapproche de celle contenue dans le manuscrit soumis. Les frais de publication pourront ne pas être débités aux auteurs qui n'ont pas reçu de subventions et dont le travail est d'une qualité exceptionnelle. L'auteur devra, de préférence, conserver les originaux du texte dactylographié et des figures (sauf les simili) jusqu'à ce qu'on les lui demande.

Un manuscrit est normalement soumis à deux arbitres pour évaluation, avant l'évaluation finale par un rédacteur. Cependant, les manuscrits qui ne répondent pas à la politique éditoriale ou à la portée du *Journal* sont retournés à l'auteur sans avoir été soumis à l'arbitrage.

## Dispositions générales

Le *Council of Biology Editors Style Manual* (5e éd., CBE, 9650 Rockville Pike, Bethesda, MD 20814) sert de guide quant à la forme de la présentation. Le *Webster's Third International Dictionary* ou l'*Oxford English Dictionary*, et le *Grand Larousse encyclopédique* font autorité pour l'orthographe des mots. L'uniformité de cette dernière est la responsabilité des auteurs. Les titres de périodiques sont abrégés suivant les *Serial Sources for the BIOSIS Data Base* (BioSciences Information Service, Philadelphia, PA 19103. C'est la responsabilité des auteurs de s'assurer que leurs références sont complètes et exactes. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (4e éd. 1980), Spec. Publ. No. 12, American Fisheries Society. Toutes les mesures doivent être conformes au système métrique et, dans la plupart des cas, être exprimées en unités SI (sauf exceptions mentionnées dans un éditorial du *Journal*, vol. 40, n° 12), et se conformer au *Guide canadien de familiarisation au système métrique* CAN3-Z234.1-79 (l'Association canadienne de normalisation, 178, boul. Rexdale, Rexdale (Ont.) M9W 1R3).

On devra éviter les titres en séries. Un résumé doit accompagner chaque texte et exposer brièvement, en 175 mots ou moins, ce qui a été fait, ce qui a été découvert et les conclusions auxquelles on est arrivé.

L'auteur doit revoir les épreuves qu'on lui remet et en corriger les erreurs typographiques. *Il doit éviter de modifier le contenu du texte.*

Cinquante tirés à part sont fournis gratuitement. Des tirés à part supplémentaires peuvent être achetés au moment de la publication (un bon de commande à cet effet accompagne les épreuves).

## Préparation des manuscrits

### Directives générales

La marche des manuscrits à travers les diverses étapes de l'arbitrage et de la révision sera grandement facilitée si les

articles sont préparés dans le style et le format du *Journal*. En cas de doute sur des points particuliers, veuillez consulter une livraison récente du *Journal*. On trouvera ci-dessous des directives générales.

Dactylographiez le manuscrit sur papier blanc, mesurant de préférence 21,5 sur 28 cm (8,5 sur 11 pouces), sur un côté de la page. Si possible, employez un papier avec lignes numérotées en marge. Laissez toujours une marge d'au moins 2,5 cm.

Sur la première page, dactylographiez le titre, les noms et affiliations des auteurs et les renvois qui s'y rapportent. Numérotez toutes les pages, à commencer par la page-titre, de même que celles contenant les tableaux et les légendes des illustrations.

Tout le manuscrit, y compris tableaux, légendes des tableaux et des figures, renvois et liste de références, doit être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique.

En aucun endroit du manuscrit n'écrivez entièrement en majuscules.

Pour les références citées dans le texte, utilisez le système nom et année.

### Liste de contrôle pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes aux buts de l'étude ?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons ? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou à l'intérieur du texte ? Est-ce que certaines données devraient être présentées séparément dans un rapport manuscrit ou dans un dépôt de données ?

Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la recherche ? Dans des énoncés de probabilité, seuls les tests statistiques sont-ils cités, et les tableaux statistiques inutiles sont-ils exclus ?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie ? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité ? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction ?

Le *titre* est-il représentatif du contenu du rapport ? Le *résumé* donne-t-il l'essentiel des connaissances nouvelles ? L' *introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude ? La revue de la littérature se limite-t-elle à la définition du problème ? La section *matériel et méthodes* contient-elle le minimum de détail qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données ? Les généralisatons sur les *résultats* sont-elles adéquates ? Permettent-elles de distinguer entre constatations et déductions ? La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes ?

Sont énumérés ci-dessous des façons d'éviter les problèmes techniques les plus communs dans la soumission des manuscrits. En accordant une attention particulière à ces points lors de la préparation de leurs manuscrits, les auteurs peuvent accélérer le traitement des articles.

1) Insérez la bande bibliographique avant le résumé (auteurs, data, titre, Can. J. Fish. Aquat. Sci.)

2) Limitez le résumé à un paragraphe d'environ 175 mots.

3) Dactylographiez à double interligne tous les éléments du manuscrit, y compris les références et les légendes des tableaux et des figures.

4) Évitez partout l'emploi exclusif de majuscules, y compris dans les en-têtes et les légendes des tableaux et des figures.

5) Ne soulignez que les noms latins d'organismes et certaines notations statistiques et mathématiques, qui devront être imprimés en italique.

6) Dans les figures, les tableaux et le texte, exprimez les unités de mesure par leurs symboles SI propres. Pour les nombres inférieurs à l'unité, placez un zéro avant la virgule décimale.

7) Évitez les formes ambiguës, telles que g C/m$^2$/d ; utilisez plutôt g C$\cdot$m$^{-2}\cdot$d$^{-1}$.

8) Identifiez le test qui a servi à évaluer la signification statistique, donnant également la valeur de probabilité. S'il s'agit de tests communs, il n'est pas nécessaire d'en donner la référence.

9) Dans le texte, généralisez à partir des tableaux et des figures ; évitez une répétition de tous les détails. Assurez-vous que chaque tableau et figure sont indépendants et que, dans le texte, on y réfère dans l'ordre numérique. Les legendes doivent indiquer le but du tableau ou de la figure.

10) Préparez la section des remerciements au stade du manuscrit et non quand vous parviennent les épreuves.

11) En référant à des communications personnnelles, donnez les initiales et l'adresse postale de la personne en cause.

12) Éliminez toutes références inutiles qui ne s'appliquent pas directement au problème.

13) Vérifiez soigneusement les références en regard des citations dans le texte et vice versa, afin de vous assurer qu'il y a correspondance. Dans le cas de matériel difficilement accessible, indiquez l'endroit où le trouver, p. ex., disponible auprès du Département de l'économique, Université Simon Fraser, Burnaby (C.-B.) V5A 1S6.

14) Éliminez les virgules entre le nom et la date dans les citations telles que (Smith 1900) et soulignez *et al.*

15) Dans les en-têtes de tableaux et les axes des figures, remplacez $10^n$ par les préfixes SI appropriés ou utilisez des mots en clair (p. ex. milliers).

16) Aux fins de la révision, les photocopies des figures, sauf les similis, sont appropriées. Sur demende, lorsqu'il s'agira de publier l'article, envoyez des photographies des digures, ou encore les originaux, s'ils ne dépassent pas 21,5 sur 28 cm. Utilisez autant que possible un lettrage uniforme.

## Parties du manuscrit

### Organisation

Organisez le manuscrit par rapport au but ou à la portée de l'étude, tels qu'énoncés dans l'introduction. Il est particulièrement important que le titre et les sous-titres soient en harmonie avec les objectifs.

Avant de commencer la rédaction du manuscrit, dressez une liste provisoire des sous-titres ou en-têtes, avec le moins de divisions possible. Retouchez-les jusqu'à ce qu'ils semblent assurer, pour le lecteur, une marche logique ; ordinairement, l'ordre chronologique ne sera pas satisfaisant. Il sera plus facile d'évaluer les résultats si vous décrivez méthodes, résultats et discussion dans des sections séparées.

Organisez les tableaux et les figures de façon à faciliter les comparaisons, groupant les données apparentées en aussi peu de tableaux et de figures que possible. Assurez-vous que ces derniers sont aussi clairs que possible sans référence au texte.

Commencez les sections et les paragraphes par des énoncés généraux qui aboutissent naturellement à des énoncés particu-

liers. Si vous donnez d'abord une conclusion que vous appuyez ensuite, non seulement votre travail sera plus facile à lire, mais aussi les autres scientifiques pourront plus aisément en évaluer les résultats. Dans la rédaction des manuscrits, le défaut le plus commun est d'omettre de donner, au début, les généralités les plus dignes de mention.

Voyez à ce que le matériel de chaque section soit pertinent à l'en-tête et que le matériel de chaque paragraphe se rapporte à la première phrase introduisant le sujet.

Avant de rédiger les paragraphes, composez la phrase-thème de chaque paragraphe et disposez ces phrases dans l'ordre approprié.

### Titre

Limitez le titre à ce que le travail veut démontrer. C'est la clé de l'article, et il devrait montrer clairement et de façon concise ce qui est contenu dans le travail lui-même. Le titre a deux fonctions : (1) il permet au lecteur de juger si, oui ou non, l'article peut avoir un intérêt et (2) il devrait fournir suffisamment d'information pour permettre au lecteur de juger de la portée et de l'importance possible de l'article. Les mots du titre devraient fournir un maximum d'information et identifier la nature de la recherche, de l'organisme utilisé et, au besoin, la méthode d'approche technique (p. ex. rayons X, chromatographie, analyse mathématique). Les titres ne devraient pas commencer par un chiffre ou par des prépositions d'introduction telles que « Sur » ou « Vers », ou des expressions telles que « Contribution à ... » ou « Recherches sur ... ». De bons titres facilitent le classement des publications et leur utilisation par les scientifiques et les bibliothécaires.

### Résumé

Le résumé doit refléter succintement le contenu et les points principaux de l'article en 175 mots environ. Comme le titre, le résumé permet aux lecteurs de prendre connaissance du contenu de l'article et de décider si, oui ou non, il leur faut lire ce dernier en entier. Indiquez au début du résumé la principale conclusion de l'étude et appuyez-la par des découvertes pertinentes. Ne donnez que les détails des méthodes nécessaires à la compréhension de ce qui a été fait et insérez-les dans l'énoncé des découvertes. Évitez l'emploi de phrases telles que « ... on y analyse » ou « ... a été trouvé » ; soyez spécifique. Comme le résumé est souvent séparé du corps principal de l'article par les services d'analyse et de classement, et que est c'est la seule partie d'un travail que certains lecteurs auront l'occasion de voir, il est important que le résumé reflète précisément le contenu du travail.

### Introduction

Limitez l'introduction à la portée, au but et à la raison de l'étude. Ne mentionnez que les travaux publiés et autre informations nécessaires à la définition du problème et à la perspective du travail. Commencez avec le but ou la portée du travail, définissez ensuite le problème et ajoutez ici et là des jalons qui aideront à orienter le lecteur. En général, une introduction n'a pas besoin de dépasser 375–500 mots.

### Matériel et méthodes

Cette section renferme ce dont on a besoin pour trouver réponse aux questions soulevées dans les objectifs du travail.

Limitez les renseignements à ce qui est nécessaire pour juger de la validité des découvertes. Cette évaluation sera facilitée si vous présentez, autant que possible, toute l'information dans une section. S'il s'agit d'outillage ou de techniques déjà publiés, référez à ces publications et ne décrivez en détail que les adaptations. Il y a souvent avantage à commencer un énoncé des méthodes par une phase qui en indique le but, comme : « Afin de déterminer ... nous ... » Si la section est longue, songez à utiliser des sous-titres correspondant à ceux que vous utilisez dans la section des résultats.

### Résultats

Limitez les résultats aux réponses apportées aux questions en rapport avec le but de l'étude ; que ces réponses soient aussi complètes que possibles, tout en étant concises. Exprimez ce que vous avez trouvé, autant que possible dans les mêmes termes que ceux dans lesquels les observations ou les mesures ont été faites, évitant ainsi de confondre faits et spéculations. En dégageant les généralités des tableaux et des figures, référez-y et évitez de répéter dans le texte ce que les légendes devraient exprimer clairement. Le matériel complémentaire au texte peut être classé dans les séries des rapports ou dans un dépôt de données reconnu, et on y référera dans le texte.

### Discussion

Limitez la discussion à l'énoncé de la principale contribution de l'étude et à l'interprétation de découvertes particulières, les comparant avec celles d'autres auteurs. On continuera à mettre l'accent sur la synethèse et l'interprétation, ainsi que sur l'exposition de généralisations et de principes largement applicables. S'il s'agit d'exceptions ou de points douteux, notez-les et faites ressortir la manière dont vos résultats corroborent ou contredisent les travaux déjà publiés. Limitez la spéculation à ce que vous pouvez appuyer sur des preuves raisonnables. Terminez cette section par un court résumé de l'importance du travail et des conclusions auxquelles il a conduit. Si la discussion est brève et précise, elle peut être combinée avec les résultats en une seule et même section.

### Remerciements

Nous recommandons fortement aux auteurs de limiter les remerciements aux personnes qui ont contribué d'une manière substantielle aux aspects scientifiques et techniques de l'article, fourni une aide financière ou amélioré la qualité de la présentation. Évitez de mentionner les personnes qui n'ont fourni qu'un travail de soutien.

### Références

On choisira les références avec soin, les limitant aux publications importantes. On ne peut citer dans cette section les références à des données inédites, manuscrits en préparation ou soumis à d'autres périodiques, états des travaux at communications inédites présentées à des réunions annuelles. On peut toutefois les mentionner dans le texte à titre de données inédites ou de communications personnelles (les adresses incluant). Si l'on doit citer des rapports d'experts-conseils ou d'autres documents dont la distribution est limitée, on devra préciser l'encroit où l'on peut se les procurer. On doit s'assurer que les références mentionnées dans le texte correspondre à celles qui sont contenues dans la liste de références et vice versa. Presque tous les manuscrits soumis au *Journal* contiennent des erreurs dans cette section.

## Tableaux

Les tableaux sont utilisés pour présenter des données qui se répètent et devraient occuper le moins d'espace possible.

Agencez les tableaux de façon qu'ils s'adaptent soit à une ou deux colonnes du *Journal*.

Dactylographiez chaque tableau sur une page séparée et numérotez-les en chiffres arabes.

Tracez des lignes horizontales de part et d'autre des en-têtes et au-dessous des colonnes, mais rarement ailleurs. N'utilisez jamais de lignes verticales. Laissez plutôt des espaces supplementairies.

Chaque tableau doit avoir une légende instructive, complète et indépendante.

Les renvois des tableaux doivent être indiqués par des petites lettres suscrites dactylographiées au bas du tableau.

Placez les tableaux après la liste des références.

Quand on réfère à un tableau pour la première fois, on indique dans la marge du manuscrit « Tableau — près d'ici ».

Notez que les *tableaux dans le texte* ne sont pas numérotés et sont dactylographiés dans le corps du texte. Ils ont rarement besoin de lignes horizontales.

## Figures

Fournissez des photographies ou les dessins originaux (pourvu qu'ils ne dépassent pas 21,5 sur 28 cm) de chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas sur l'illustration même. Transmettez deux photocopies des dessins au trait et deux séries de photos qui serviront au moment de la révision.

Les dessins devront occuper une largeur de 1, 1½ ou 2 colonnes du *Journal*. Assurez-vous que tous les chiffres, lettres et symboles sont lisibles, clairs et mesurent au moins 1,5 mm de hauteur une fois réduits. Les figures ne devraient pas être montées, brochées ou fixées à l'aide de trombones. Autant que possible, elle devraient être groupées et préparées avec le même type de lettrage.

Dactylographiez les légendes, dans l'ordre, sur des feuilles séparées. Dans le cas de cartes, photomicrographies, diagrammes d'instruments, etc., ajoutez une échelle.

À l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge « Fig.— près. d'ici ».

On devra autant que possible éviter les illustrations préparées par ordinateur, qui ne se reproduisent pas très bien. Les imprimantes par points ne peuvent produire de lignes solides suffisamment foncées pour être lisibles. On obtiendra toujours de meilleurs résultats en utilisant de l'encre de Chine noire. Si vous utilisez du lettrase instantané, veillez à ce qu'il adhère parfaitement.

Il vaut mieux dessiner que dactylographier les inscriptions relatives aux axes.

La production de planches en couleurs est très dispendieuse et on ne devrait utiliser celles-ci que lorsque les couleurs sont essentielles à la compréhension du texte. Les coûts supplémentaires de reproduction de planches en couleurs sont ordinairement débités à l'auteur. Pour les reproductions en couleurs, ne soumettez que des photos d'excellente qualité. Nous préférons utiliser des photographies en couleur, mais acceptons dessins, négatifs, diapositives ou positifs de films en couleurs.

## Expressions, équations et formules mathématiques

Laissez trois espaces au-dessus et au-dessous des lignes portant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous des équations et des formules. Placez chaque composante des différentes expressions dans la position qui lui est propre.

Indiquez clairement tous les symboles. Épelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

## Abréviations

N'abrégez les termes désignant les unités de poids et mesures dans le texte que lorsqu'ils sont précédés d'un nombre.

| | |
|---|---|
| an | an |
| année | a |
| becquerel | Bq |
| calorie | cal |
| centimètre | cm |
| centimètre carré | $cm^2$ |
| centimètre cube | $cm^3$ |
| centimètre par gramme par seconde | $cm \cdot g^{-1} \cdot s^{-1}$ |
| coulomb | C |
| décimètre | dm |
| degré Celsius | °C |
| degrés de liberté | dl |
| écart type | EcT |
| élecronvolt | eV |
| erreur type | ErT |
| farad | F |
| gramme | g |
| hectare | ha |
| hertz | Hz |
| heure | h |
| joule | J |
| jour | d |
| kilomètre | km |
| litre | L |
| lumen | lm |
| lux | lx |
| mètre | m |
| mètre carré | $m^2$ |
| mètre cube | $m^3$ |
| micromètre | µm |
| milligramme | mg |
| millilitre | mL |
| millimètre | mm |
| millimètre carré | $mm^2$ |
| minute | min |
| mois | mo |
| masse molaire | *M* |
| mole | mol |
| pascal | Pa |
| seconde | s |
| semaine | sem |
| tonne | t |
| volt | V |
| volume | vol |
| watt | W |

## Dates

On écrira les dates dans l'ordre jour–mois–année, p.ex. 9 octobre 1983, sans virgule entre le mois et l'année.

## Citations de références dans le texte

*Système de nom et année*

Le *Journal* utilise le système de nom et année, c.-à-d. que le nom de l'auteur ou des auteurs et l'année de publication sont insérés dans le texte à un endroit approprié: «Brown (1983) compare ...» ou «... on a comparé (Brown 1983)». Si la référence comporte plus de deux auteurs, inscrivez le nom du premier auteur seulement, suivi de « *et al.*» : «Brown *et al.* (1983) comparent ...» ou «... on a comparé (Brown *et al.* 1983)».

*Communications personnelles*

Les communications personnelles ne doivent pas être incluses dans la liste des références. Utilisez plutôt des parenthèses dans le texte, entre lesquelles vous indiquerez le nom et l'adresse de la personne en question, suivis de «comm. pers.»

*Données inédites*

Si le livre ou l'article inédits ont été acceptés pour publication, insérez-les dans la liste des références, avec la mention «(Sous presse)». On ne peut considérer comme étant sous presse que les manuscrits au stade d'épreuves ou ceux couverts par lettre d'acceptation. Si l'article a été soumis mais n'a pas encore été accepté, ne l'incluez pas dans la liste de références, mais indiquez le nom et l'adresse de l'auteur du matériel inédit, dans le texte lui-même, avec la mention « données inédites ».

## Liste de références

La liste qui suit donne des exemples de ponctuation, de style et d'abréviations utilisés dans les références bibiographiques (d'aprés les *Serial Sources for the BIOSIS Data Base*).

*Article du journal*

ARCHAMBAULT, D ET E. BOURGET. 1983. Importance du régime de dénudation sur la structure et la succession des communautés intertidales de substrat rocheux en milieu subarctique. Can. J. Fish. Aquat. Sci. 40 : 1278–1292.

*Numéro complet du journal*

GORDON, D. C., JR. ET A. S. HOURSTON [ÉD.] 1983. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40 : (Suppl. 1) : 1–365.

*Livre dans une série*

HILTON, J. W. ET S. J. SLINGER. 1981. Nutrition et alimentation de la truite arc-en-ciel. Publ. spéc. can. sci. halieut. aquat. 55 : 17 p.

*Livre ne faisant pas partie d'une série*

FORRESTER, W. D. 1983. Manuel canadien des marées. Ministère des Pêches et des Océans, Service hydrographique du Canada, Ottawa (Ont.). 148 p.

*Partie d'un livre*

AUBERT, M., J. AUBERT, S. DANIEL ET N. DESIROTTE. 1972. État actuel de la pollution bactérienne au large des côtes françaises, p. 36–40. *Dans* M. Ruivo [éd.] La pollution des mers et les ressources biologiques. Fishing News (Books) Ltd., Londres.

*Corporation-auteur*

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION ET WATER POLLUTION CONTROL FEDERATION. 1975. Standard methods for the examination of water and wastewater. 14$^{e}$ éd. Washington, DC. 1193 p.

*Thèse*

DELISLE, C. 1969. Écologie, croissance et comportement de l'éperlan du Lac Heney, Comté de Gatineau ainsi que la répartition en eau douce du Québec. Thèse doctorale, Univ. Ottawa, Ottawa (Ont.). 161 p.

*Rapports*

DUTIL, J. D., M. FORTIN ET Y. VIGNEAULT. 1982. L'importance des zones littorales pour les ressources halieutiques. Mémoire remis au Conseil consultatif de l'environnement du Québec. Rapp. manus. can. halieut. aquat 1653 : 29 p.

*Traduction*

KOIKE, A. ET M. OGURA. 1977. Selectivity of meshes and entrances of shrimp traps and crab traps. J. Tokyo Univ. Fish. 64 : 1–11. (Traduit du japonais par Can. Transl. Fish. Aquat. Sci. 4950, 1983)

## Temps

On devra séparer par deux points (:) heures et minutes, et minutes et secondes. Les symboles «h», «min» et «s» ne seront pas utilisés car ils représentent heure, minute et seconde dans le sens de durée ou intervalle de temps. C'est ainsi que «12 h 30 min» exprime un intervalle de temps de douze heures et trente minutes, alors que 12:30 se rapporte à l'heure du jour.

## Liste de mots

Cette section, dans la version anglaise du Guide, contient une série de mots dont l'orthographe pose certains problèmes d'uniformité, comme, par exemple, «cold water» (n.), «cold-water» (adj.) ; «hard water» (n.), «hardwater» (adj.), etc. L'auteur préparant un texte en anglais est prié de consulter la version anglaise du Guide.

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Journal canadien des sciences halieutiques et aquatiques

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